Limnological and Biological Observations in the Region of the Ungava or Chubb Crater, Province of Quebec[1]

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ABSTRACT

Ungava Crater Lake, at 73° 41′ W.L. and 61° 17′ N.L., lies in a meteoritic crater of the northern Quebec tundra. The lake is nearly circular, 1.7 miles in diameter, with steep walls and a maximum known depth of 825 feet. Secchi disc transparency was 35 metres. Summer surface temperatures were 3–4° C., of the deep water a little less. Surface oxygen was abundant, pH was 6.5–6.6. Total solids in the water were less than 20 parts per million, and hardness was only 1.7 p.p.m. Three kinds of mammals and 14 of birds were found in the crater region. Arctic char, *Salvelinus alpinus*, were the only fish taken in the crater lake. Specimens up to 21.8 inches fork length and 18 years old were taken; they fed on insects and other char. Char in other nearby waters grew somewhat faster but ate the same foods; mature females as small as 4.0 inches were seen. Lake trout, *Salvelinus namaycush*, in a lake near the crater reached 33.5 inches and 15.8 pounds. Growth was very slow, the greatest age determined being 21 years, at 13 pounds. Twenty-nine species of vascular plants were collected close to the crater.

INTRODUCTION

From July 25 to August 20, 1951, a National Geographic Society–Royal Ontario Museum expedition investigated the Ungava (Chubb) Crater in northern Quebec. A description of the crater and its geological significance may be found in articles by Meen (1950, 1951, 1952) and Harrison (1954). The crater is meteoritic, originating some time before the last advance of continental ice. One of the secondary aims of the expedition was a survey of the limnology and biology of the crater and surrounding areas.

Ungava Crater is located at 73° 41′ west longitude and 61° 17′ north latitude on a rolling plateau at an altitude of about 2,200 feet. The headwaters of the Povungnituk and Payne Rivers virtually encircle the crater (Fig. 1).

Rousseau (1952) has classified the country in Quebec north of 59° N.L. as typically tundra and notes that the tundra reaches farther south in Ungava than anywhere else in the world. Ungava Crater is approximately 200 miles beyond the timber line.

LIMNOLOGICAL OBSERVATIONS

Ungava Crater Lake

morphometry. Figure 2 is a photograph of the crater. Nearly two-thirds of the circular crater depression is filled with a lake 1.7 miles in diameter and

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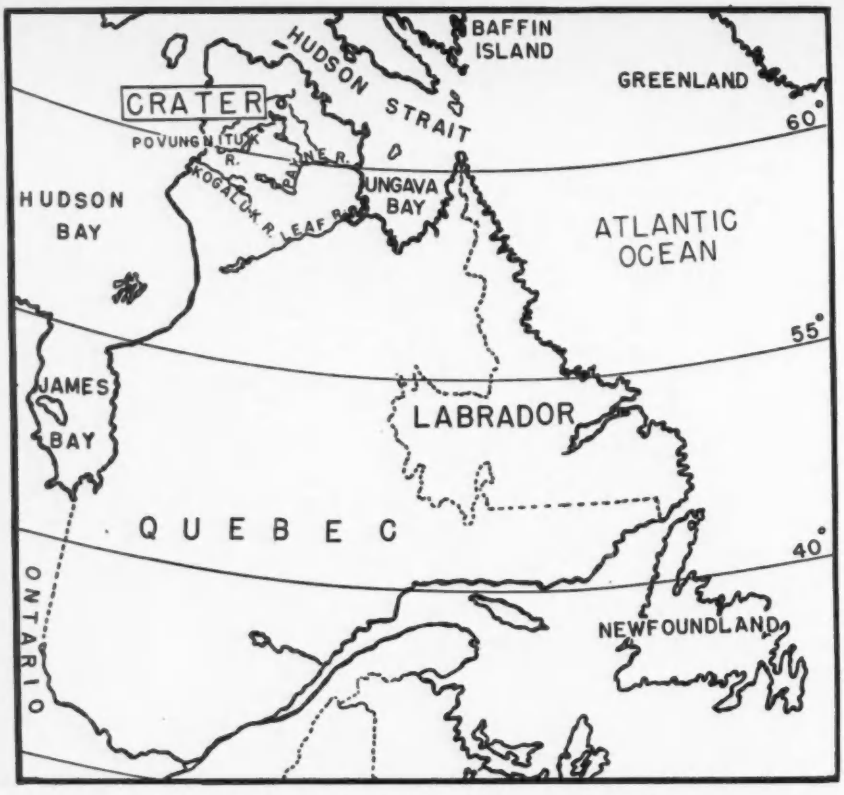

FIGURE 1. Map showing location of Ungava Crater, Quebec.

FIGURE 2. Ungava Crater from the west. The high point on the rim on the far side of the crater is 550 feet above the lake surface. Note the ponds on the crater flanks. (Photograph courtesy of the National Geographic Society.)

2.3 square miles in extent. There is no obvious connection between this lake and surrounding drainages.

The basin of the lake is symmetrical, with steep slopes approximating those of the crater wall above water (up to 45°). The maximum depth found in 17 soundings was 825 feet, and because of the steepness of the slopes the lake is 500 feet or more deep over 80 per cent of its surface.

TEMPERATURE. Temperature readings on July 31 were 2.9°C. at the surface and 2.6°C. from 9 feet to 400 feet. Surface temperature on August 18 was 3.9°C.

OXYGEN. Surface readings for oxygen values were taken on July 31 (14.4 p.p.m.) and August 11 (15.2 p.p.m.). Unfortunately there are no deep water oxygen values as the water bottle was lost while taking the first oxygen series.

HYDROGEN ION CONCENTRATION. A La Motte comparator was used in making the pH determinations. Surface readings in the crater lake were 6.5 on July 31 and 6.6 on August 11.

TRANSPARENCY. A standard Secchi disc was used to measure water transparency. A reading of 115 feet (35 metres) was obtained in the crater lake on August 11 under somewhat less than ideal conditions. Ungava Crater Lake is therefore one of the world's clearest lakes, its clarity being exceeded only by that of Lake Masyûko, Japan (41.6 metres) and Crater Lake, Oregon (40 metres).

MINERAL CONTENT. A gallon of water was taken for mineral analysis (Table I). Ungava Crater Lake has one of the lowest values for dissolved solids reported for any lake. The silicate and sodium values are probably too high because the sample was stored in a glass bottle before analysis.

The analysis of this water was made by the Department of Public Health, Province of Ontario, and Miss Papson of the Ontario Department of Lands and Forests.

TABLE I. Mineral analysis of surface water taken from Ungava Crater Lake, Quebec, August 18, 1951, in parts per million.

Total solids	less than 20.0	Aluminum	1.60
Organic matter (loss on ignition)	less than 15.0	Calcium	less than 1.00
		Sodium	0.30
Hardness	1.70	Potassium	less than 0.02
Alkalinity	1.20	Magnesium	less than 0.10
Nitrogen as N	0.83	Silicate	2.40
Nitrite	0.00	Sulphate	0.70
Nitrate	0.08	Chlorides	0.00
Iron	less than 0.04	Phosphorus	less than 0.001

OTHER LAKES

Miscellaneous observations on other lakes (Fig. 3) are included in Table II.

Air temperatures in the July 25 to August 20 period ranged from a low of 26°F. to a high of 65°F., with a mean figure of approximately 41°F. Precipitation in the region is low and has been estimated to be less than 10 inches per year.

TABLE II. Summary of limnological observations on lakes other than Ungava Crater Lake.

Lake	Approximate maximum depth	Surface temperature	Bottom temperature	pH (surface)	Oxygen (surface)	Secchi disc value
	feet	°C.	°C.		*mg/l*	*feet*
Museum	30	Aug. 16 7.8	Aug. 16 8.4	Aug. 4 6.4	...	...
North Pond	27	...	...	Aug. 11 6.6	Aug. 11 10.8	Aug. 11 17
West Pond	...	Aug. 20 3.9	...	...	...	...

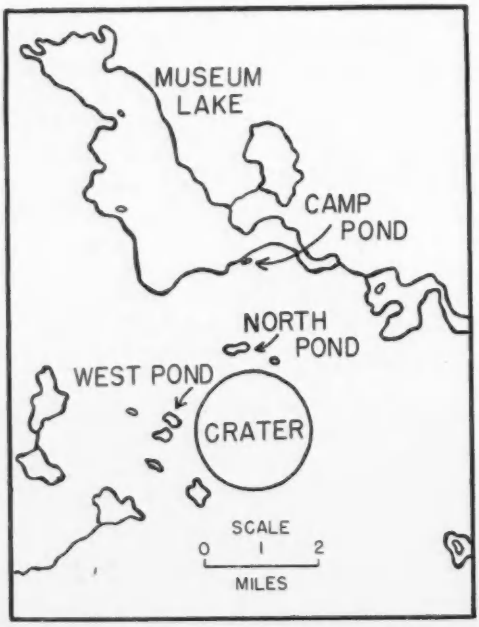

FIGURE 3. Details of the immediate crater region showing neighbouring ponds and lakes.

BIOLOGICAL OBSERVATIONS

Unfortunately some parts of the biological collections were accidentally destroyed. This includes the collection of plants, insects, plankton, bottom fauna dredgings, stomach contents of fish and miscellaneous lesser items.

MAMMALS

Only two species of mammals and three individuals were observed during the stay at the crater. Two arctic fox, *Alopex lagopus ungava*, and one Labrador

varying lemming, *Dicrostonyx hudsonius*, were collected. In addition the Richardson's ermine, *Mustela erminea richardsoni*, was identified from snowy owl pellets. Weathered skeletal remains and antlers of the barren ground caribou, *Rangifer caboti*, were common, though this species is now rare in Ungava.

Further evidence of the scarcity of mammal life in the crater region was the failure of small mammal traps to capture a single specimen. There was also little indirect evidence such as droppings, tracks or burrows.

Identification of the material was made by Dr. R. L. Peterson of the Royal Ontario Museum of Zoology and Palaeontology, Toronto.

Birds

Birds seen in the crater region were common loon, red-throated loon, herring gull, arctic tern,* semipalmated sandpiper, semipalmated plover, golden plover, rock ptarmigan, duck hawk,* golden? eagle, horned lark, snow bunting,* lapland longspur,* and pipit.*

Identification of the specimens brought back was made by the late C. E. Hope of the Royal Ontario Museum; they are indicated by an asterisk above.

Fishes

UNGAVA CRATER LAKE. Fish were taken from the crater lake by angling (4 fish) and minnow trapping (7 fish). Only one species was taken, the arctic char, *Salvelinus alpinus* (Fig. 4, Table III).

Small char and aquatic and terrestrial insects were found in the stomachs of these specimens. Growth was extremely slow. Two of the large char were quite emaciated (Fig. 4). From the examination of the gonads of these char and those taken from other lakes it is evident char in this region do not spawn every year.

FIGURE 4. A 20-inch arctic char taken from Ungava Crater Lake.

TABLE III. Length, age, sex, and food of arctic char taken from Ungava Crater Lake, Quebec.

Fork length	Age	Sex and maturity	Stomach contents
inches	*years*		
21.8	18	Mature ♀	Fish remains
20.0	14	Mature ♂	Insects
18.8	14	Mature ♀	Three char, insects
17.5	13	Mature ♂	Insects
3.2	1	Immature ♀	Empty
3.1	1	Immature	Insect trace
3.0	1	Immature	Insect trace
2.2	0	Immature	Insect trace
2.0	0	Immature	Insects
1.9	0	Immature	Empty
1.7	0	Immature	Insect trace

TABLE IV. Length, age, sex, and food of arctic char taken from North Pond, Ungava Crater region, Quebec.

Fork length	Age	Sex and maturity	Egg count	Stomach contents
inches	*years*			
19.8	13	Mature ♂	...	Empty
18.9	11	Mature ♀	...	Fish remains
18.3	...	Immature ♂	...	Empty
17.4	9	Mature ♀	...	Insect trace
15.6	9	Mature ♂	...	Fish remains; insects
15.4	10	Immature ♂	...	Insects
15.2	10	Immature ♂	...	Fish remains
14.3	12	Mature ♂	...	Empty
11.1	8	Immature ♂	...	Empty
9.1	7	Immature ♀	...	Empty
7.0	4	Immature ♀	...	...
5.0	4	Immature ♀	...	Insects
4.4	3	Immature ♂	...	Insect trace
4.3	2	Ripe ♀	21	Empty
4.0	2	Ripe ♀	41	Insects
4.0	2	Immature ♂	...	Insects
3.8	2	Immature ♂	...	...
3.8	2	Mature ♂	...	Insects
3.7	2	Mature ♂	...	Empty
3.6	2	Immature ♀	...	Insects
2.8	1	Immature	...	...
2.6	1	Immature	...	...
2.6	1	Immature	...	...
2.6	1	Immature	...	...
2.6	1	Immature	...	...
1.9	0	Immature	...	...

NORTH POND. North Pond is located part way up the northern flank of the crater (Fig. 3). Arctic char were taken from this pond by gill-netting (11) and minnow traps (43).

The stomach contents of these fish were similar to those of the crater char (Table IV). Age determinations by the scale method were difficult and the figures for the older fish can only be regarded as approximations. Growth of the North Pond char appears somewhat faster than that of the crater fish.

Pond char first mature at about 4 inches in length and two years of age. In the small sample no mature fish were taken between 3 and 10 years of age. Two-year-old char produced less than 50 eggs per female.

The viscera of the larger fish were heavily parasitized with plerocercoid cysts of Diphyllobothridae.

CAMP POND. Camp Pond (Fig. 3) is a shallow pond less than an acre in extent separated from Museum Lake by a low gravel bar. Arctic char and lake trout, *Salvelinus namaycush*, were collected from this pond after an application of rotenone. At least 90 per cent of the population of approximately 200 fish in the pond were arctic char. Data on a sample of this collection are shown in Table V.

TABLE V. Length, age, sex, and food of arctic char and lake trout taken from Camp Pond, Ungava Crater region, Quebec.

Fork length	Age	Sex and maturity	Egg count	Stomach contents
inches				
		LAKE TROUT		
4.4	3	Immature♂	...	Empty
3.1	2	Immature	...	...
		ARCTIC CHAR		
5.2	2	Ripe♀	202	Insect trace
4.9	2	Ripe♂	...	Empty
4.7	3	Ripe♀	113	Empty
4.6	3	Ripe♀	98	Fish remains
4.2	2	Ripe♂	...	Cladocera
4.1	2	Ripe♂	...	Empty
4.1	2	Ripe♀	...	...
4.0	2	Ripe♀	94	Crustacea
3.8	2	Ripe♀	...	...
3.7	2	Ripe♂	...	...
3.7	...	Ripe♂	...	Empty
3.5	2	Maturing♀	...	Cladocera
3.2	1	Immature♀	...	...
3.1	1	...	...	...
3.1	1	Immature♀	...	Insects
3.1	1	Immature♀	...	Empty
3.0	1	Immature♀	...	...
3.0	2	Ripe♂	...	...

In food, growth and time of maturity these char were similar to North Pond char. Camp Pond char appeared to spawn every year. Egg counts were two to five times greater than with the North Pond char.

MUSEUM LAKE. Both arctic char and lake trout were taken in Museum Lake by angling, gill-netting, seining, and minnow traps. Only two large char were taken as compared with about 50 lake trout. As an indication of the abundance of these species, one 150-foot length of gill net set for one night in 4 to 8 feet

TABLE VI. Length, weight, age, sex and food of lake trout taken from Museum Lake, Ungava Crater region, Quebec.

Fork length	Weight	Age	Sex and maturity	Stomach contents
inches	*ounces*			
32.6	208	21	...	...
32.5	252	...	Mature♂	1 large fish; insects
32.2	...	21	...	3 fish
25.9	...	19	...	...
25.3	92	...	...	...
24.9	86	...	Mature♀	Fish
24.8	88	...	Immature♂	...
24.7	94	...	Mature♀	Insect trace; 1 fish
22.4	69	...	Mature♂	...
22.4	...	18	...	...
21.6	59	17	...	...
20.0	44	...	Immature♀	Insect trace
19.5	42	15	Immature♂	...
19.3	41	15	Mature♂	...
19.1	37	13	Immature♂	Insects
18.8	...	15	...	...
18.8	44	11	...	...
18.6	39	16	Immature♂	...
18.4	41	15	Mature♀	Insects
18.2	...	15	Immature♂	Insects
17.9	55	13	Immature♂	...
17.8	...	...	Mature♂	Insects
17.4	...	15	Mature♀	Insects
17.3	30	...	Immature♀	...
17.2	28	...	...	...
17.2	28	14	Immature♀	...
16.6	...	13	Immature♂	1 lake trout; insects
16.6	...	14	Mature♂	1 lake trout; insects
16.5	...	11	Immature♂	Insects
16.5	...	...	Mature♂	Insects
16.5	28	13	Immature♂	Insects
16.3	27	12	Mature♂	...
16.1	21	12	Immature♂	...
15.7	...	12	Mature♂	Insects
14.8	21	12	Immature♂	...
14.1	17	12	Immature♂	Fish remains; insects
10.8	...	9	Immature♀	Insects
2.0	...	...	Immature♀	1 lake trout; insects

of water took 9 lake trout. Another set for two nights took 10 lake trout and 2 char.

Data on fish collected in Museum Lake are in Table VI. Lake trout food at this time was fish and insects. Most of the insect food was at the surface, on the aerial stages of aquatic forms or the adults of terrestrial species. There was little feeding on aquatic stages and none on bottom-living forms.

The size of the trout collected ranged up to 33.5 inches and 15.8 pounds. These fish were well conditioned and the length-weight curve is comparable with that of lake trout in more temperate and productive waters. Growth of the Museum Lake trout is extremely slow. On the basis of the data collected it is similar to that of Great Bear Lake trout (Miller and Kennedy, 1948) which have the slowest growth on record. Some of the trout mature by 12 years of age. They do not appear to spawn every year.

Many of the trout were infested with plerocercoid cysts (Diphyllobothridae) and the parasitic copepod, *Salmincola* sp., was noted on the fins of some lake trout.

Dr. W. B. Scott, Royal Ontario Museum of Zoology and Palaeontology, made the identification of the fish material.

Crustaceans

Two species of Branchiopoda were taken from West Pond. Although this material was destroyed before final identification had been made, one was known to be a fairy shrimp (Anostraca) and the other belonged to the genus *Lepidurus* (Notostraca). A cladoceran, *Eurycerus* sp. was found in the stomachs of the char in Camp Pond.

Insects

Some indication of the insects present in the crater region was obtained from the stomach contents of the char and trout collected from the crater lake, North Pond, and Museum Lake.

Plecoptera: adult Nemouridae

Trichoptera: pupae and adults of *Radenna* sp.

Lepidoptera: adult moths

Diptera: adult Tipulidae; pupae, larvae and adults of Chironomidae (*Chironomus*); adults of Syrphidae (*Eristalis*); adults of Tachinidae; adults of Muscoidea.

Coleoptera: adults of Dytiscidae

Hymenoptera: adult Chalcidoidea; adult Ichneumonidae.

Plankton and Bottom Fauna

Vertical and horizontal tows with a closing net indicated that plankton was sparse in the crater lake but abundant in North Pond. Museum Lake appeared to be intermediate between these two in plankton abundance.

A six-inch Ekman dredge, modified by the addition of a flat iron ring as developed by Rawson (1947), was used in the bottom fauna sampling. This

failed to take any dredgings in the crater lake although used up to depths of 450 feet.

Dredging in Museum Lake was also unsuccessful because of the hard nature of the bottom. In North Pond there was a rich population of chironomid larvae in the bottom muds.

ACKNOWLEDGMENTS

The author wishes to thank Dr. V. B. Meen, expedition leader, for his generous allotment of time and facilities to the carrying out of the biological work. The assistance of Mr. F. Chubb and Mr. R. H. Stewart in the field investigations is gratefully acknowledged.

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APPENDIX: THE FLORA OF CHUBB CRATER

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Situated in the arctic zone of the Quebec-Labrador Peninsula, the region of Chubb Crater certainly possesses the poorest flora in the Province of Quebec. The fact that the district is covered by the thick layer of boulders with little or no surface soil increases the drainage and renders the general habitat a particularly dry one.

The senior author paid a visit, lasting but a few hours, to the Crater on August 15, 1951. The stop-over did not permit the author more than to proceed from the base camp to the crater. Mr. N. V. Martin, the biologist of the field-party on location at the site, had already made a collection of plants. Since it was impossible to undertake a complete survey of the flora in the very short time at his disposal, the senior author concentrated his efforts on filling the gaps in the collection already made. Notwithstanding, he was able to collect anew a large number of species contained in Martin's collection, which was all to the good since the material collected by Martin was accidentally destroyed after reaching its destination.

The list presented below contains only the plants brought back plus one other species shown in the photographs taken. It was not found advisable to complete this list by making a call upon memory: too many odd records in phytogeography stem from such a source, memory being none too reliable.

Consequently the list of vascular plants below (29 species) makes no claim to being an exhaustive one of the flora, though it is safe to affirm that it is not far from being so. Probably no more than ten species may eventually be added to the enumeration. Among them, one may cite a couple of *Pedicularis* species and probably *Dryopteris fragrans.*

One must note the fact that shrubs are almost completely absent. For instance, the willow collected was not the only species seen but was the only specimen growing in the area covered. Outside the plants listed hereunder, the senior author has also collected lichens, liverworts, mosses (including *Rhacomitrium lanuginosum*), algae (including *Sphaerella nivalis* which forms red patches on snow), fungi and soil bacteria. These collections are being studied by various specialists in those groups who will publish their findings later on.

Antennaria angustata Greene (det. A. E. Porsild)

Antennaria Ekmaniana A. E. Porsild (id.).—According to Dr. Porsild, the most arctic member of this genus. From northern West Greenland, it reaches the Bering Strait across the arctic islands. See map in Porsild, *Can. Field-Nat.*, **64**: 8, 1950. Its southernmost locality is in the Ungava-Labrador Peninsula.

Arctagrostis latifolia (R. Br.) Griseb.

Campanula uniflora L.

Cardamine bellidifolia L.

Carex Bigelowii Torr., f. *glacialis* (Fries) Raymond—This is the dwarf extreme of a wide-ranging variable species. It seems to be what Holm has described as *C. Fyllae* in *Bot. Jahrb.*, **8**: 294, 1887, the type (or an isotype) of which the junior author has had occasion to examine in the Herbarium of the British Museum.

Cassiope tetragona (L). D. Don

Cerastium alpinum L.—This is only a provisionary determination: our arctic Cerastia are sorely in need of revision.

Draba lactea Adams—It seems advisable to treat this as a species rather than as *Draba fladnizensis* Wulf., var. *heterotricha* (Lindblom) Ball.

Epilobium latifolium L.

Festuca brachyphylla Schultes

Lycopodium Selago L.

Eutrema Edwardsii R. Br.

Hierochloe alpina (Sw.) R. & S.

Luzula arctica Blytt—Many names have been applied to this very neat and easily distinguishable arctic species, the oldest and valid one being Blytt's, in *Norges Fl.*, I: 299, 1861. For a detailed history, see Hylander, *Uppsala Univers. Arsskr.*, 1945, no. 7, p. 108.

Luzula confusa Lindeberg

Oxyria digyna (L.) Hill
Papaver radicatum Rottb.—An odd type of this most variable circumpolar species, closely approaching ssp. *hyperboreum* Nordhagen, and probably already described in one of the innumerable taxa created by Fedde.
Pedicularis lapponica L.
Potentilla hyparctica Malte
Pyrola grandiflora Radius
Ranunculus pedatifidus Sm., var. *leiocarpus* (Trautv.) Fernald
Salix anglorum Chamisso (det. C. R. Ball)
Salix herbacea L.
Saxifraga cernua L.
Saxifraga rivularis L.
Silene acaulis L., var. *exscapa* (All.) D.C.
Stellaria crassipes Hultén
Trisetum spicatum (L.) Richt.

On the Ecology of Skeena River Whitefishes, *Coregonus* and *Prosopium*[1,2]

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ABSTRACT

Incidental information on the ecology of the common (Eastern) whitefish, *Coregonus clupeaformis*, and the Rocky Mountain whitefish, *Prosopium williamsoni*, was collected in the course of the Skeena River Salmon Investigation of 1944–1948. The common whitefish has been found in only four Skeena lakes, which have characteristics that are mainly oligotrophic. Rocky Mountain whitefish were taken in all the lakes where netting was done, which included warm and shallow, as well as deep and cold, bodies of water. The bottom fauna of Lakelse, Babine and Morrison Lakes was described. During the summer common whitefish were most abundant in depths of 10–15 m., and Rocky Mountain whitefish at 5–10 m. The food of the two species was very similar, and consisted mostly of bottom organisms. An exception was that of common whitefish in Morrison Lake, which had fed almost wholly upon plankton crustaceans. This situation was associated with the paucity of bottom fauna in the lake. The important competitors for food of the whitefishes, identified on the basis of common food and habitat, were peamouth chub, *Mylocheilus caurinum*, and squawfish, *Ptychocheilus oregonense*. Chief predators of the whitefish were lake trout, *Cristivomer namaycush*, and ling, *Lota lota*. However, there was no evidence that predation upon either

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whitefish was particularly serious. The oldest common whitefish were X years of age (473 mm. fork length), and Rocky Mountain whitefish IX years (365 mm. fork length). No food organisms occur in the Skeena lakes in such abundance as do certain amphipods in other Canadian lakes where the common whitefish is fished commercially. This scarcity of suitable food is considered to be the main condition limiting the abundance of the Skeena populations of common whitefish.

INTRODUCTION

During 1944–1948 the Fisheries Research Board of Canada conducted an investigation of the salmon populations of the Skeena River (Pritchard, 1949), in the course of which incidental information was obtained on the general ecology of other fishes inhabiting the Skeena lakes, including the common whitefish, *Coregonus clupeaformis* (Mitchill), and the Rocky Mountain whitefish, *Prosopium williamsoni* (Girard).

Most information comes from three lakes, Babine, Morrison and Lakelse, where field research parties operated during much of each summer in 1944–1948. Other lakes were visited for only very brief periods, and in some cases only once during the course of the investigation. For this reason the data presented here, which deal with lake bottom fauna, the depth distribution, food habits and the competitors and predators of the whitefishes, are for the three lakes only. The conditions described pertain only to the summer months.

The common whitefish is widely distributed over the North American continent. In the Great Lakes, and in large prairie and northern lakes, it occurs in such abundance as to contribute to Canada's most important freshwater fishery. The species is sometimes anadromous, as, for example, in the Hudson Bay region (Dymond, 1933), and in the Alaskan Arctic (Wynne-Edwards, 1952). It occurs in the Yukon, the Northwest Territories, and in northern British Columbia west of the Rocky Mountains; it has also been introduced into lakes of southern British Columbia (Carl and Clemens, 1953).

In contrast to the common whitefish, the Rocky Mountain whitefish is restricted mainly to regions west of the Rocky Mountains (although, according to Radforth, 1944, it has crossed this barrier at certain points), and in British Columbia to more southerly lakes and streams (Dymond, 1936; Carl and Clemens, 1953). In recent years its known northward distribution has been extended through record of its occurrence in lakes of the Fraser and Skeena River systems.

The scientific names of fishes mentioned in this paper (including tables) are given below. Common and scientific names are according to Carl and Clemens (1953), except for a few emendations of spelling.

Ling	*Lota lota*
Dolly Varden char	*Salvelinus alpinus malma*
Lake trout	*Cristivomer namaycush*
Rainbow trout	*Salmo gairdneri*
Cutthroat trout	*Salmo clarki*
Peamouth chub	*Mylocheilus caurinum*
Squawfish	*Ptychocheilus oregonense*
Fine-scaled sucker	*Catostomus catostomus*

White sucker	*Catostomus commersoni*
Coarse-scaled sucker	*Catostomus macrocheilus*
Sculpin	*Cottus asper*
Three-spined stickleback	*Gasterosteus aculeatus*
Redside shiner	*Richardsonius balteatus*
Lake chub	*Couesius plumbeus greeni*
Longnose dace	*Rhinichthys cataractae*
Redbelly dace	*Chrosomus eos*
Kokanee	*Oncorhynchus nerka kennerlyi*

THE SKEENA LAKES

A map of the Skeena system is shown in Figure 1. The area of the drainage is approximately 19,3000 sq. mi. In the north it arises in the Kluayaz-Duti River systems at 57°12′ N. Lat., 127°45′ W. Long., and extends approximately 245 miles

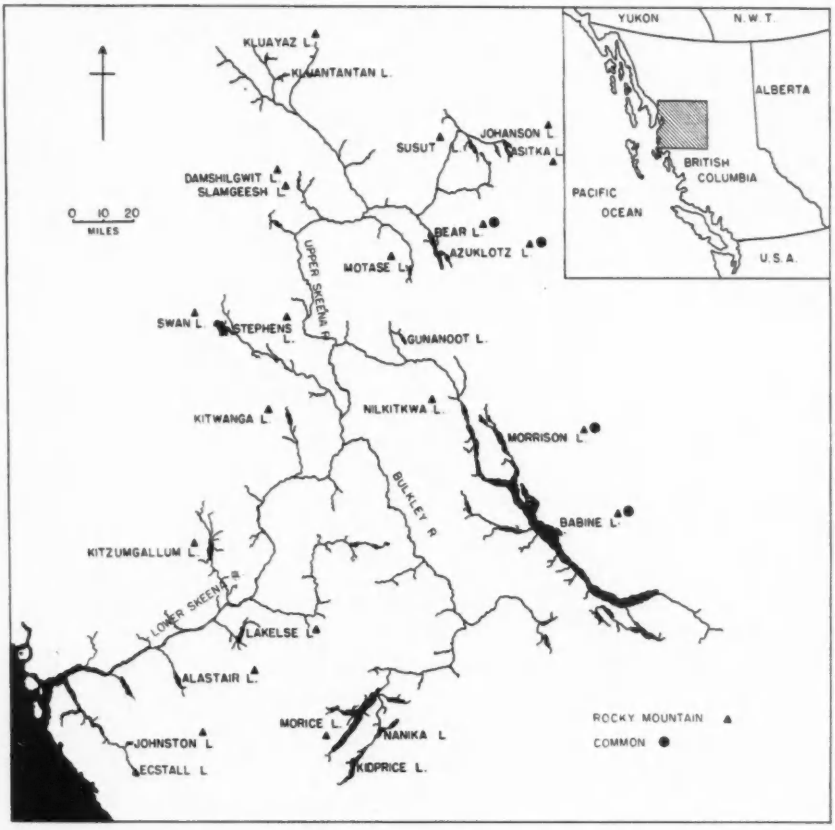

FIGURE 1. Map of the Skeena River showing the known distribution of the common and the Rocky Mountain whitefishes.

TABLE I. Some morphological and physico-chemical characteristics of 20 Skeena lakes.

	Alastair	Lakelse	Kitsumgallum	Kitwanga	Swan	Stephens	Morice	Babine	Nilkitkwa	Morrison
Area—*sq. mi.*	2.3	5.5	6.8	2.8	10.8	3.1	40.0	171.8	2.0	5.6
hectares	596	1417	1761	725	2797	803	10360	44496	518	1450
Max. length—*km.*	8.4	8.7	10.9	6.9	11.3	5.6	41.7	148.8	10.5	15.3
Max. width—*km.*	0.8	2.4	2.6	1.6	3.2	1.6	4.5	9.3	0.8	1.8
Max. depth—*m.*	71.9	29.9	132.6	13.4	64.0	25.9	236.2	207.3	18.9	61.0
Mean depth—*m.*	22.6	7.3	70.9	7.3	22.9	10.4	99.7	49.1	5.8	20.7
Volume—*cu. m.* × 10^6	139.6	108.0	1247.8	52.0	636.1	85.6	10327.5	26551.5	29.8	305.8
Shoreline development	2.2	1.8	2.0	2.3	3.5	2.1	3.2	6.6	2.8	2.6
Elevation—*feet*	500	220	468	600	1500	1500	2614	2322	2310	2400
metres	153	67	143	183	459	459	797	708	705	732
Surface peak temperature—°C.	17.1	20.2	18.0	19.1	...	20.3	...	18.3	18.4	18.4
Bottom peak temperature—°C.	4.4	13.8	4.0	7.0	4.3	5.0	4.0	7.5	8.6	5.4
Mean summer transparency[a]—*m.*	7.9	3.1	0.5	5.8	...	...	3.0	5.8	4.9	3.4
Min. summer bottom O_2, % saturation	...	45	80	...	90	72	...	52	63	62

	Slamgeesh	Damshilgwit	Motase	Azuklotz	Bear	Sustut	Johanson	Kluayaz	Johnston	Asitka
Area—*sq. mi.*	...	...	...	...	7.2	1.3	0.6	...	0.9	...
hectares	...	...	...	...	1865	337	155	...	225	...
Max. length—*km.*	0.4	...	5.6	2.8	20.0	5.6	4.4	3.2	3.2	1.2
Max. width—*km.*	0.4	0.4	1.6	1.2	4.8	0.8	0.8	1.6	1.0	0.8
Max. depth—*m.*	7.9	12.2	32.0	10.7	73.2	18.6	49.4	19.5	...	7.9
Mean depth—*m.*	...	...	...	...	12.8	6.4	14.6	...	...	...
Volume—*cu. m.* × 10^6	...	...	...	...	240.0	21.4	22.9	...	...	...
Shoreline development	...	...	...	...	3.2	2.1	2.9	...	...	...
Elevation—*feet*	...	...	3350	2648	2640	4250	4730	3800	...	4250
metres	...	...	1022	808	805	1296	1443	1159	...	1296
Surface peak temperature—°C.	11.5	11.8	8.8	18.8	19.3	...	11.5	11.3	...	13.5
Bottom peak temperature—°C.	11.4	8.9	6.3	16.2	6.0	...	5.3	7.8	...	11.7
Mean summer transparency[a]—*m.*	3.7	3.7	0.2	4.4	4.4	9.1	9.1	0.2	...	5.5
Min. summer bottom O_2, % saturation	...	...	...	...	...	...	...	...	...	...

[a]Depth of Secchi disc visibility.

TABLE II. Conditions for eutrophy and oligotrophy in 10 Skeena lakes.

	Lakelse	Babine	Morrison	Kitwanga	Kitsum-gallum	Alastair	Swan	Stephens	Morice	Bear
Depth	shallow	deep	medium	shallow	deep	medium	medium	shallow	deep	medium
Area	small	large	small	small	small	small	small	small	large	small
Bottom shape	V	U	V	V	U	V	V	V	U	V
Thermally stratified	occasional	no	yes	...	no	yes	yes	yes	no	yes
Temperature	high	low	high	high	low	low	high	high	low	high
Bottom oxygen concentration	high	high	high	low	high	...	high	high	high	high
pH in summer	not low	not low	not low	not low	not low	...	not low	not low	not low	not low
Plankton abundance	moderate	low	moderate	high	low	moderate	moderate	high	low	moderate
Bottom fauna abundance	moderate	low	low	...	...	...	...	...	...	...
Silted	no	no	no	no	yes	no	no	no	yes	no
Eutrophic or oligotrophic	E	O	O	E	O	O	O	E	O	O

to its southern limit in the Nanika Lake district of the Morice River system, at 53°40′ N. Lat., 127°50′ W. Long. It originates in the east from the headwaters of the Sutherland River, a small tributary to Babine Lake, at 54°15′ N. Lat., 124°40′ W. Long., and extends westward for approximately 220 miles to the mouth of the river, on the Pacific Coast, at 54°10′ N. Lat., 130°10′ W. Long. The highest lake in the Skeena drainage is Johanson Lake, at 4,730 feet elevation. Between Hazelton and Prince Rupert the river transects the range of coastal mountains. More than 75 per cent of the Skeena drainage lies within the central plateau, east of the Coast Mountains, at elevations greater than 2,000 feet.

Skeena lakes have been described in the following publications: Kitsumgallum Lake (Brett, 1946); Kitwanga Lake (McConnell and Brett, 1946); Morice Lake (Brett and Pritchard, 1946); Lakelse Lake (Brett and Pritchard, 1946; Brett, 1950); Sustut, Asitka, Johanson, Darb and Spawning Lakes (Foskett, 1947); Bear Lake (Foskett, 1947); Swan, Club and Stephens Lakes (Withler, 1948); Morrison Lake (McMahon, 1948); Babine Lake (Withler *et al.*, 1949).

Some morphological and physico-chemical characteristics of 20 Skeena lakes (including 8 for which no descriptions have been published) are listed in Table I. In Table II are listed the conditions of depth, area, bottom contour, temperature, thermal stratification, bottom oxygen concentration, pH of water in summer, abundance of plankton and bottom organisms, and degree of silting of water. By means of these data 10 of the more important Skeena lakes have been classified as of the eutrophic or oligotrophic types, following the generally accepted criteria (cf. Rawson, 1930, 1934, 1939 and 1942).

Although not all of the lakes are consistent in every respect, they are conveniently divided as follows: eutrophic—Lakelse, Kitwanga and Stephens; oligotrophic—Babine, Morrison, Kitsumgallum, Alastair, Swan, Morice and Bear.

Other Skeena lakes are classified tentatively as: eutrophic—Nilkitkwa; oligotrophic— Johnston, Motase, Kluayaz, Sustut and Johanson; Azuklotz Lake was surveyed only very briefly, and has characteristics of both these types.

Some of the northern Skeena lakes appear to be in a dystrophic phase, with the accumulation of humic materials, and the encroachment of marginal plants and their incomplete decay. Such lakes are Slamgeesh, Damshilgwit and Astika.

OCCURRENCE OF THE WHITEFISHES IN THE SKEENA SYSTEM

Skeena lakes in which either or both of the whitefishes are known to occur are indicated in Figure 1. Table III also lists their known distribution in the Skeena together with that of several other Skeena fishes. The common whitefish has been taken in only four Skeena lakes—Babine, Morrison, Bear and Azuklotz. The first three are oligotrophic, while Azuklotz Lake has characteristics of both types (Table I).

Since some of the Skeena lakes were investigated only very briefly, fish collections from them may not have been complete. No common whitefish were found in Morice or Nilkitkwa Lakes where a fair number of sets of gangs of gill-nets were made. Since Babine Lake empties into Nilkitkwa Lake by way of the 2-mile long Upper Babine River, the common whitefish probably does occur

TABLE III. The known occurrence of fishes in Skeena lakes, adapted from Withler (1948). Fishing effort is in terms of number of gangs of gill-nets set: A = more than 50 gangs; B = 20–50 gangs; C = 10–19 gangs; D = 5–9 gangs; E = less than 5 gangs.

	Alastair	Lakelse	Kitsumgallum	Kitwanga	Swan	Stephens	Morice	Babine	Nilkitkwa	Morrison	Slamgeesh	Damshilgwit	Motase	Azuklotz	Bear	Sustut	Johanson	Kluayaz
Fishing effort: No. of gangs set	E	A	D	D	D	D	C	A	C	A	E	E	E	D	B	E	E	E
Common whitefish								x		x				x	x			
Rocky Mountain whitefish	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Peamouth chub	x	x	x	x				x	x	x								
Squawfish		x		x				x	x	x								
Cutthroat trout	x	x	x	x				x	x	x								
Dolly Varden char	x	x	x	x	x	x	x				x	x	x	x	x	x	x	
Rainbow trout		x			x	x	x	x	x	x	x	x			x	x	x	
Northern sucker	x	x		x	x	x	x	x		x	x		x	x	x			x
White sucker				x			x	x	x	x					x			
Coarse-scaled sucker		x																
Burbot								x	x	x				x	x	x		
Lake trout							x	x	x	x					x			
Kokanee				x				x		x	x				x	x		

in Nilkitkwa Lake temporarily. Extensive netting has never taken the common whitefish in Lakelse Lake. In the remaining Skeena lakes, although the sampling effort has at times been meagre, it is certain that they were not supporting large populations of this fish.

Rocky Mountain whitefish are the most widely distributed of the Skeena fishes. They have been found, and usually in fair abundance, in every Skeena lake investigated. They have also been observed in numerous rivers and streams within the system. The lakes in which these fish have been caught vary from deep, cold and opaque bodies of water, to small, shallow and warm ponds.

BOTTOM FAUNA OF LAKELSE, BABINE AND MORRISON LAKES

METHODS AND MATERIALS

An Ekman dredge was used to obtain bottom samples from Babine, Morrison and Lakelse Lakes. The dredge sampled an area of 484 sq. cm. Contents of the dredge were washed successively through square screens of ¼-inch wire, $\frac{3}{32}$-inch wire, and $\frac{1}{16}$-inch cotton. The screened organisms were preserved in 5 per cent formalin and examined later.

Limitations of the technique of bottom sampling with the Ekman dredge have been described by Rawson (1930). Primarily, they result from the unevenness of the bottom, leakage as the dredge is hauled up, loss of organisms

during screening, and the non-uniform distribution of organisms over the bottom.

In Lakelse Lake, 73 dredge hauls were made in 1945 during the period July 5 to September 5, along 12 lines which were chosen to sample representatively the different depths and habitats. In Babine Lake, in July of 1946, 41 dredgings were made in three widely separated regions of the lake (Divisions I, II and III). Altogether, 9 hauls were made at depths of 25–100 m., and 30 hauls at depths of 1–10 m. One sample was taken at 15 m., and one at 20 m. Only 12 samples were collected from Morrison Lake (in 1946 and 1947), along two widely separated lines at depths ranging at 1-m. intervals from 1 to 5 m.; additional samples were taken at 8, 10 and 20 m.

Lakelse Lake

(1) depth zones

In Lakelse Lake three types of zones are referred to which are identified by their depths. These are the littoral (0–5 m.), the sub-littoral (5–15 m.) and the profundal (deeper than 15 m.).

Eggleton (1939) defines the littoral zone as the region that lies between the shoreline and the approximate lakeward limit of rooted aquatic vegetation; the profundal, as the region which extends from the greatest depths, up the slope to a level somewhat above that corresponding to the average limit of the hypolimnion; and the sub-littoral as the region lying between the littoral and the profundal. These definitions are similar to those of Welch (1935).

Characteristics of the profundal zone, as given by Eggleton, are: a permanently low temperature; lack of dissolved oxygen in some parts; acidity of water at times; little or no light; and, often, an accumulation of carbon dioxide, methane or other gases of decomposition. It does not follow any sharp transition from the sub-littoral.

The sub-littoral zone is described by Eggleton as a zone of "heaping refuse", and as the "shell zone", because of the accumulation of dead mollusc shells. It is a zone of transition from the conditions of the littoral to those of the profundal.

Although Lakelse Lake does not conform altogether to Eggleton's zonal classification, that system is conveniently used here for the following reasons. Rooted aquatic vegetation in most of Lakelse Lake is abundant down to depths of 5 m., and is sparse or absent at greater depths. The 0–5–m. zone can therefore be referred to as the littoral. A depression which provides the lake's maximum depth of 32 m. is situated near the north end, and the occasional thermoclines which occur in the lake were found only in this region; in late summer the limit of the hypolimnion was at 20 m., approximately. Temperatures in this deep water have been permanently low (although at 24 m. they have reached 7.3°C.). The lowest oxygen concentration recorded was 45 per cent saturation, at 25 m. Little or no light penetrates to this depth in Lakelse Lake. In relation to the overall characteristics of the lake, therefore, this deep-water region may be conveniently referred to as the profundal.

(2) ABUNDANCE AND DEPTH.

A total of 2,653 organisms was collected from the 73 hauls (Table IV). The order of the abundance of organisms was: Pelecypoda, Amphipoda, Gastropoda, Ephemeridae (nymphs), Chironomidae (larvae), Oligochaeta and Trichoptera (larvae). The remaining forms constituted only 3.6 per cent of the total number.

The depth distribution of the six most important groups of organisms is shown in Figure 2. The zone of greatest abundance lay between the shoreline and a depth of 5 m.—that is, within the littoral zone. Here the concentration of the more important fauna was approximately 1,045 per sq. m. In the sub-littoral zone there were 180 per sq. m., and in the profundal zone approximately 311 per sq. m.

TABLE IV. Bottom fauna in Lakelse Lake. Collections from 73 dredge hauls, 1946.

Organisms	Total no. in 73 hauls	Av. no. per dredge	Av. no. per sq. metre	Percentage of total
Total	2,653	36.3	751	...
Pelecypoda	715	9.8	203	27
Hyalella	523	7.2	149	20
Gastropoda	502	6.9	143	19
Ephemerida—nymph	388	5.3	110	15
Chironomid—larva	189	2.6	54	7
Oligochaeta	135	1.8	37	5
Trichoptera—larva	106	1.5	31	4
Hirudinea	38	...	...	...
Odonata—nymph	17	...	...	...
Diptera—larva	13	...	...	...
Mysis	6	...	...	...
Cyclostomata—lamprey	5	...	...	...
Hydracarina	3	...	...	...
Hemiptera	3	1.3	27	4
Fish larvae	3	...	...	...
Arachnida	2	...	...	...
Hymenoptera	2	...	...	...
Coleoptera—adult	1	...	...	...
Insecta—larva	2	...	...	...

(3) DISTRIBUTION OF ABUNDANT FORMS

PELECYPODA. The Pelecypoda in the lake consisted mostly of the genera *Pisidium* and *Sphaerium*, of the family Sphaeridae. They occurred in most habitats and at all depths (Fig. 2), but were found most frequently in mud and sand, in the vicinity of pond weeds. The maximum occurrence of pelecypods was in the littoral zone, at a mean depth of 2.5 m. Their number fell to a minimum in the sub-littoral, and remained fairly constant from there to the deepest water.

GASTROPODS. Most of the gastropods were very small species of the genus *Planorbis* (s. l.). They were in greatest abundance in the littoral zone, at a mean

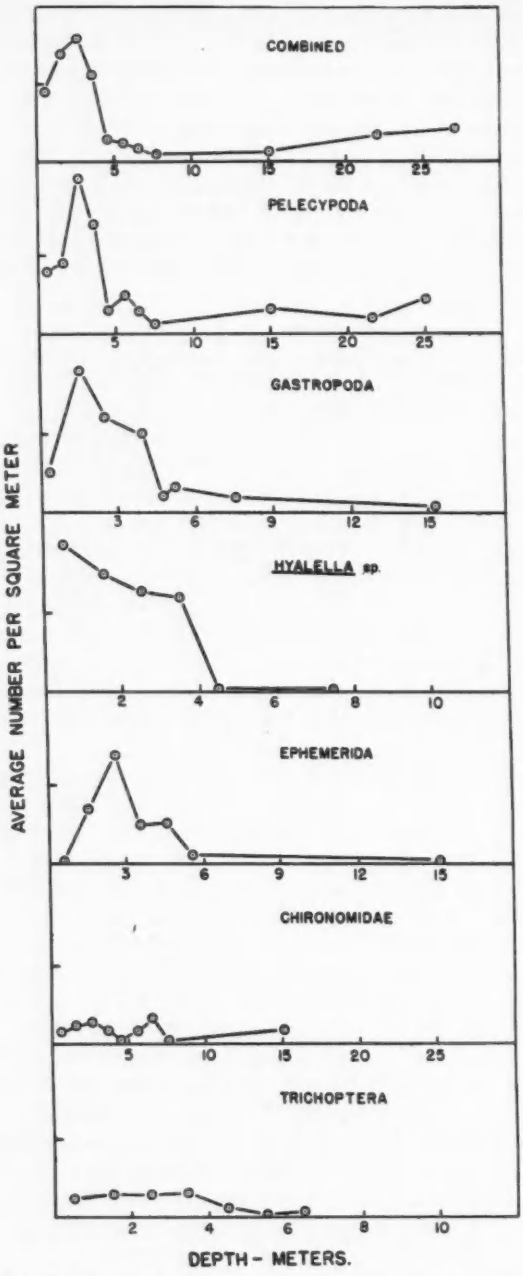

FIGURE 2. Depth distribution of the 6 major groups of bottom organisms in Lakelse Lake, 1945.

depth of 1.5 m. (Fig. 2). Like the pelecypods, they were scarce in the sub-littoral: none was found in depths greater than 15 m.

Hyalella sp. This was the only genus of the Amphipoda found. *Hyalella* was not collected from depths exceeding 7 m., and was rare at depths greater than 4 m. It was commonest close inshore, at an average depth of less than 2 m. (Fig. 2). *Hyalella* was found in muddy bottom, and particularly in areas bearing pond weeds.

EPHEMERIDA. Almost all the mayfly nymphs belonged to the burrowing type of the genus *Ephemera*. They were most abundant at a depth of 2.5 m.; very few were found in water shallower than 1 m. (Fig. 2). Only a few nymphs were found in the sub-littoral. One specimen was found from among the few hauls in the 15–m. zone.

CHIRONOMIDAE. Chironomidae larvae and the Pelecypoda were the only organisms of the six major groups which were collected in the five hauls at depths greater than 15 m. They were most abundant in the profundal zone; were sparsely distributed in the littoral and sub-littoral zones, with only small

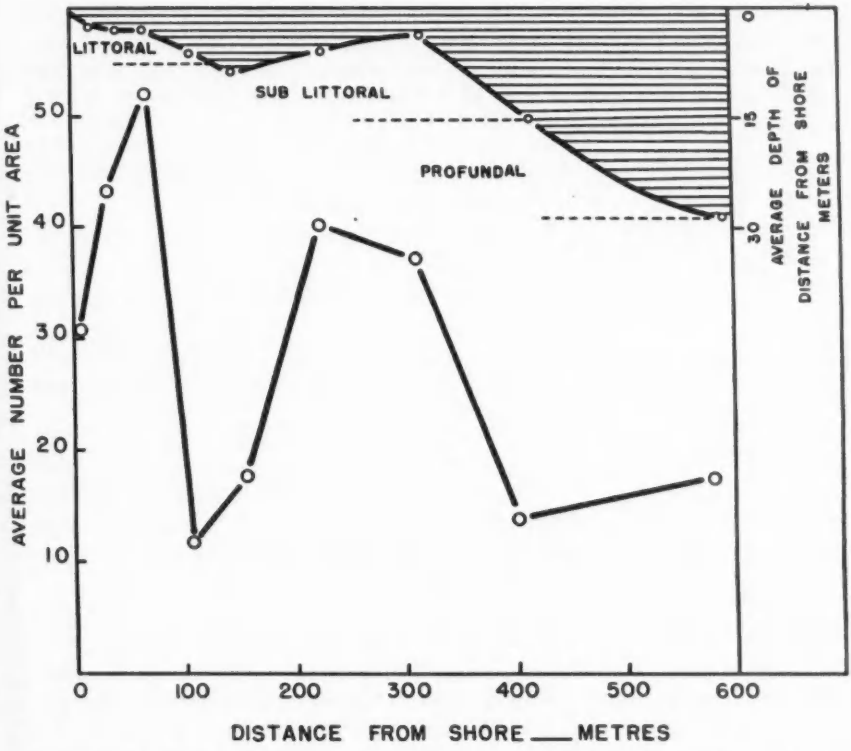

FIGURE 3. The relative abundance of bottom organisms in Lakelse Lake at different distances from shore, and the average depths at such distances, 1945.

differences between the two. It was the Chironomidae which contributed most to the increase of total fauna from the sub-littoral to the profundal (Fig. 2). This distribution is apparently characteristic of certain of the chironomids.

TRICHOPTERA. Although their cases were also collected frequently, only the actual larvae have been included in the Trichoptera counts. They were distributed quite evenly down to depths of 4 m. (Fig. 2), but nowhere were they particularly abundant. They were less abundant in the sub-littoral zone, and none was collected from depths greater than 7 m.

OTHER ORGANISMS. In addition to the organisms listed in Table IV, Algae, Bryozoa (mostly statoblasts), and the freshwater sponge, *Spongilla*, were frequently taken in hauls.

(4) ABUNDANCE AND DISTANCE FROM SHORE

The average number of organisms at varying distances from shore has been plotted in Figure 3. Peaks of abundance occurred at approximately 70 and 230 m. from shore. The mean depths of these distances were 5 m. or less. The fewest organisms were found at distances of 100 and 400 m., whose mean depths were between 5 and 15 m., that is, corresponding to the sub-littoral. At distances of between 450 and 600 m. the number of organisms increased slightly; these distances had mean depths of 15 to 28 m., corresponding to the profundal zone. Thus, the abundance of organisms on the bottom of the lake appears to have been related to depth, rather than to distance from shore.

(5) ABUNDANCE AND AREA

The areas of the three depth zones in Lakelse Lake were as follows:

0– 5 m. – 612 ha. or 2.35 sq. mi.	– Littoral zone
5–10 m. – 396 ha. or 1.53 sq. mi.	– Sub-littoral zone
10–15 m. – 207 ha. or 0.80 sq. mi.	
15–20 m. – 153 ha. or 0.59 sq. mi.	– Profundal zone
20–25 m. – 49 ha. or 0.19 sq. mi.	
25–30 m. – 3 ha. or 0.01 sq. mi.	

The littoral zone constituted approximately 43 per cent of the lake's total area, and was, therefore, equal to the area of the sub-littoral. The area of the profundal was about 14 per cent of the total area of the lake.

Considering all the organisms collected, they occurred in the three zones as follows: littoral, 1,112 per sq. m.; sub-littoral, 244 per sq. m.; profundal, 317 per sq. m. The weighted average for the whole lake was therefore 628 organisms per sq. m. Employing averages which have been weighted for area of depth zones, then, 76 per cent of the organisms were in the littoral, 16 per cent in the sub-littoral, and 8 per cent in the profundal.

BABINE LAKE

Table V summarizes the collections made in the three widely separated regions of the lake, which are referred to as Divisions I, II and III. The unweighted average of all collections was only 453 organisms per sq. m., which is indicative of the poor abundance for the lake as a whole. The variety of organisms

TABLE V. Bottom fauna in Babine Lake. Collections from 41 dredge hauls, 1946.

	Average number of organisms per dredge					
	Div. I	Div. II		Div. III		All divisions
	Line I	Line I	Line II	Line I	Line II	All lines
Hyalella	6.6	5.0	...	1.0	0.9	2.3
Chironomidae (larvae)	3.2	2.4	0.6	2.9	8.6	3.7
Trichoptera (larvae)	0.4	...	0.1	0.4	0.1	...
Ephemerida (nymphs)	0.2	0.1	0.1	0.4	0.1	0.2
Coleoptera (adult)	...	...	0.1	...	...	T
Plecoptera (adult)	...	...	...	0.1	...	T
Diptera (larvae)	...	...	...	1.1	0.6	T
Gastropoda	12.8	2.4	1.3	12.1	13.4	8.0
Pelecypoda	1.8	5.0	0.7	6.8	8.6	5.0
Oligochaeta	0.6	1.3	0.1	1.1	3.1	1.4
Hemiptera	0.2	...	...	0.1	...	T
Hirudinea	0.2	0.3	...	0.4	2.0	T
Archnida	...	...	...	...	0.1	T
Fish—larvae	...	0.1	...	...	...	T
Hydracarina	...	...	...	...	0.4	T
No. of dredgings analysed	5	9	9	8	10	41
Total no. of organisms	130	150	27	212	379	898
Av. no. per dredge	26.0	16.7	3.0	26.5	37.9	21.9
Av. no. per sq. metre	538	346	62	549	785	453
Av. depth of lines—*metres*	4.8	26.7	22.2	11.3	5.9	15

in Babine and Lakelse Lakes was quite similar, but there were marked differences in the abundance of certain forms. In Babine Lake the Gastropoda were more numerous than the Pelecypoda, particularly in the shallower zones of Divisions I and II. Mayfly nymphs and caddis larvae were scarce. The greatest abundance of organisms was in the 0–5–m. zone.

Because of the small number of dredge hauls made in the lake, only a few general computations of the distribution of the bottom fauna can be made. In the 0–5–m. zone there were 683 organisms per sq. m.; 186 per sq. m. in the 5–15–m. zone; and 83 per sq. m. in the depths greater than 15 m. (Corresponding values for Lakelse Lake were 1,112, 244 and 317.)

The approximate areas of various depth zones in Babine Lake are:

0–20 m. – 11, 526 ha. or 45 sq. mi. – 26 per cent of total area.
20– 40 m. – 10,671 ha. or 41 sq. mi. – 24 per cent of total area.
40–180 m. – 22,300 ha. or 86 sq. mi. – 50 per cent of total area.

Contour lines shallower than 20 m. have not been determined, but if as much as one-half of the 0–20–m. zone belongs to the 0–5–m. zone, then the approximate weighted average abundance of benthos is $[(22.5 \times 683) + (22.5 \times 186) + (127 \times 83)] / 172$, or 175 organisms per sq. m. The paucity of bottom organisms in Babine Lake is in particular contrast to the relative wealth of bottom fauna in

certain other Canadian lakes classified as oligotrophic (Great Slave and Athabasca, for example), where bottom forms such as the amphipod *Pontoporeia* are very abundant (Rawson, 1947, a, b).

Morrison Lake

Only 12 dredge hauls were made in this lake (in 1946 and 1947). The writer was provided with a summary of the analysis of the bottom samples, which is shown as Table VI. The total number of organisms taken in the 12 hauls was only 67, or an average of 116 per sq. mi.

Much of the bottom of the lake is of a sticky, grey mud, lacking in organic matter, and this probably accounts in part for scarcity of bottom organisms. Furthermore, the 0–5–m. zone, and the 5–10–m. zone make up only 19 and 16 per cent, respectively, of the total area of the lake, so that the productive shallow area of the lake is very limited. In comparison, in Lakelse Lake those depth zones made up 70 per cent of the total area.

Table VI.. Bottom fauna in Morrison Lake. Collections from 12 dredge hauls, 1946 and 1947.

Organism	No. of species	Numbers	No. per sample
Oligochaeta	1	2	0.17
Phyllopoda	1	2	0.17
Mullusca—Gastropoda	1	5	0.41
Lamellibranchia	2	7	0.60
Insecta—Ephemeroptera	2	10	0.90
Neuroptera	2	10	0.90
Diptera	2	31	2.60

DEPTH DISTRIBUTION OF THE WHITEFISHES

Method and Materials

To obtain specimens of fish from Skeena lakes and a measure of the relative abundance of the different species, standard sets of gill-nets were made at selected positions during the summer months. Nets of different sizes of mesh were joined together in gangs, a typical gang consisting of 5 nets of 1½-, 2½-, 3½-, 4½- and 5½-inch (stretched) mesh, joined in that order. Each net of a given mesh size was 150 ft. long and 6 ft. deep, so that each gang was 750 ft. long and 6 ft. deep. The nets were supported by a line of floats, and were weighted by a bottom lead line. Gangs were anchored at both ends, so that the lead line lay along the bottom of the lake.

A standard set was made by laying a gang of nets in a standard position, either parallel to (i.e., throughout uniform depth) or perpendicular to the shore. The latter type of set was the more common, since it provided greater variety of depths fished; this was also achieved by reversing the gangs on alternate nights of fishing. Standard netting positions were chosen to include offshore slopes that varied from gradual to steep, and different kinds of habitat.

The duration of sets varied a little because of weather conditions and other factors, but all sets lasted throughout one night, and not more than one night.

Thus, a unit of effort is available, which is the "catch-per-net-night", hereinafter referred to as the C.N.N.

When the nets were hauled, each fish caught was placed in a bin identified for the size of the mesh in which it had been gilled, and that net's position in the gang. For each fish, therefore, it was possible to record where and when it had been taken, the depth of capture, and the mesh which had gilled it.

Although there was overlapping in the sizes of fish they gilled, the average size of fish increased with an increase in the size of the mesh (Tables VII and VIII); the mesh sizes will therefore be used to indicate the relative size of the fish taken. To facilitate the analysis, because nets varying by small fractions of an inch were used, mesh sizes have been grouped by mesh numbers as follows: meshes of 1 in. to and including 1½ in. as mesh No. 1; of over 1½ in. to and including 2½ in. as mesh No. 2, and so on up to mesh No. 5 for meshes of over 4½ in.

The depth distribution of fish in relation to their size has been determined upon the premises that their frequency of capture in a given depth zone reflected their relative abundance there, and that the average size of the fish caught increased with the size of the mesh in which they were gilled. A similar method was used by Hile and Juday (1941) to determine the bathymetric distribution of several species of fish in some Wisconsin lakes.

TABLE VII. Average sizes, in inches, of Rocky Mountain whitefish in nets (linen or cotton) of different size, Lakelse Lake, 1946 and 1947. (A few sets of cotton meshes of sizes 2.7-inch and 2.1-inch have been included with the 2¾- and the 2-inch meshes, respectively.)

	Mesh size in inches, stretched						
	1½	1¾	2	2½	2¾	3	3½
No. of fish	29	5	69	26	33	5	2
Av. size	8.3	10.0	9.8	11.1	12.3	13.0	13.1
Range	6.8–10.3	6.8–13.5	7.5–11.5	9.3–14.5	10.5–13.5	10.5–14.5	11.5–14.8
St. deviation	1.06	3.19	0.89	1.04	0.74	...	...

TABLE VIII. Average sizes, in inches, of common whitefish caught in nets of different size Morrison Lake, 1946 and 1947.

	Mesh size in inches, stretched						
	1½	2	2½	3	3½	4	5
LINEN NETS							
No. of fish	17	28	6	10	24	4	1
Av. size	6.9	9.5	11.8	13.1	13.2	13.6	18.0
Range	6.0–8.3	8.0–14.0	11.5–12.8	11.8–14.3	12.5–14.5	11.8–14.3	...
St. deviation	0.84	2.04	0.54	0.79	0.53	1.21	...
COTTON NETS							
No. of fish	16	20	22	45	32	5	2
Av. size	7.6	12.6	12.1	13.3	13.5	12.9	14.1
Range	5.8–8.3	11.0–14.0	8.8–14.3	11.3–14.5	12.5–14.8	11.0–13.8	13.3–15.0
St. deviation	1.53	1.35	2.02	0.77	0.62	1.10	...

COMMON WHITEFISH

(1) BABINE LAKE (Fig. 4; Table IX).

The greatest C.N.N. was made in the 10–15–m. zone; much smaller catches were made in either deeper or shallower water, but relatively more fish were caught in the 0–5– and 5–10–m. zones than in water deeper than 15 m. No fish

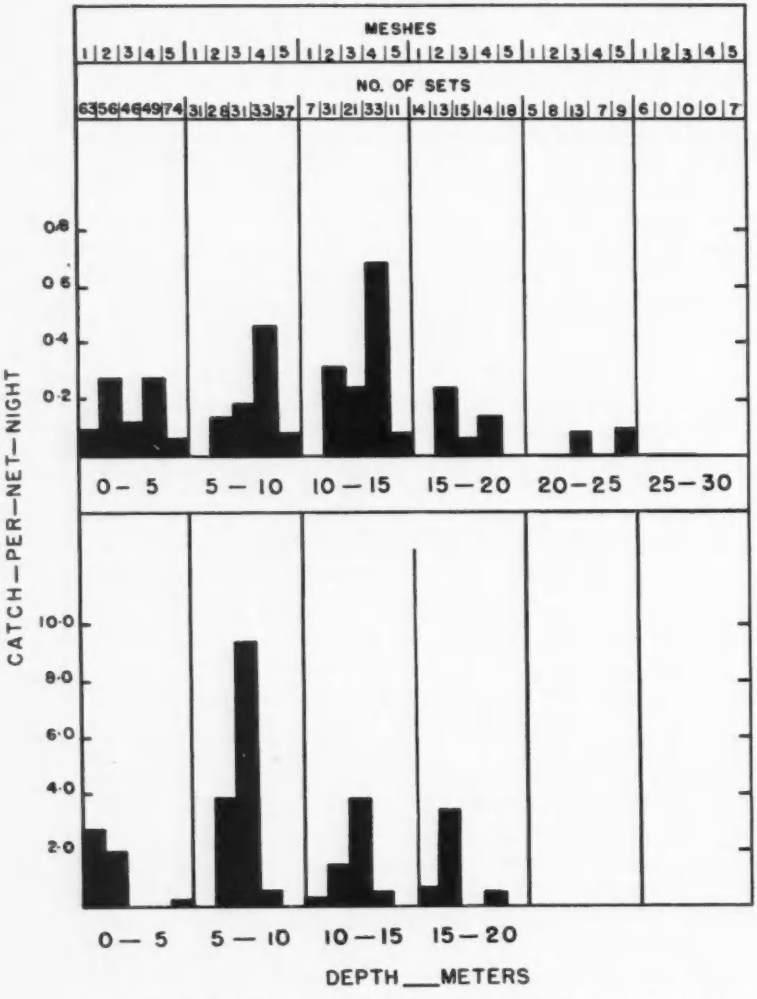

FIGURE 4. Catch-per-net-night of common whitefish at different depths in Babine (A) and Morrison (B) Lakes, 1946 and 1947.

were taken in water deeper than the 20–25-m. zone, although 13 sets were made with nets of meshes Nos. 1 and 5.

The catch did not increase directly with depth, but the largest catches were made in positions of intermediate depth:

Catch-per-net-night	*Standard position No. (and mean depth in* m.)
1.00 or greater	5 (9.8); 2 (4.0); 3 (11.6)
0.51–0.99	10 (10.1); 1 (12.2)
0.50 or less	5 (1.8); 6 (7.9); 7 (3.0); 8 (3.4); 9 (15.8)

The smallest fish, taken by meshes of No. 1 group, were caught only in the 0.5-m. zone, although these meshes were set in deeper water 63 times. Fish taken by meshes of Nos. 2, 3 and 4 groups were captured most frequently in the 10–15-m. zone. The catches of larger fish, in meshes of No. 5 group, were fairly evenly distributed from shallow water to the 20–25-m. zone.

TABLE IX. Catch-depth relationship of common whitefish in Babine Lake. Catch-per-net-night at different positions in Division II.

	Positions									
	1	2	3	4	5	6	7	8	9	10
1946	1.00	2.00	0.00	0.50	1.50	0.50	0.00	0.25	0.25	0.50
1947	0.50	0.40	1.80	0.25	1.00	0.00	0.40	0.00	0.00	1.00
Combined	0.67	1.11	1.00	0.38	1.25	0.25	0.22	0.13	0.13	0.83
Av. depth—*ft.*	40	13	38	6	32	26	10	11	52	33
Av. depth—*m.*	12.2	4.0	11.6	1.8	9.8	7.9	3.0	3.4	15.8	10.1

(2) MORRISON LAKE (Fig. 4)

Morrison Lake is a much smaller and shallower body of water than Babine Lake, and since only three standard netting positions were used, it provided a much smaller range of depths for netting. The largest catches were made in the 5–10-m. zone, with a few fish in either deeper or shallower water.

The smallest fish, taken by meshes of No. 1 group, were caught most frequently in the 0–5-m. zone, and a few were also taken in deeper water down to 20 m. Fish from mesh groups Nos. 2, 3 and 4 were most abundant at depths of 5–15 m. Only 2 large fish were taken by mesh group No. 5, and these were in the 0–5-m. zone, although 13 sets were made in deeper water.

ROCKY MOUNTAIN WHITEFISH

(1) BABINE LAKE (Fig. 5; Table X)

The greatest C.N.N. was made in the 0.5-m. zone; the catch dropped off sharply in deeper water, and no fish were taken in water deeper than the 20–25-m. zone. There was a very significant inverse relationship between the

TABLE X. Catch-depth relationship of Rocky Mountain whitefish in Babine Lake. Catch-per-net-night at different positions in Division II.

	Positions									
	1	2	3	4	5	6	7	8	9	10
1946	1.50	6.75	0.25	3.50	1.00	0.75	4.00	4.60	1.50	2.00
1947	1.50	3.20	2.40	4.00	1.75	0.25	3.50	0.00	0.50	2.75
Combined	1.50	4.78	1.44	3.78	1.38	1.38	0.50	3.71	2.56	2.17
Av. depth-*ft.*	40	13	38	6	32	26	10	11	52	33
Av. depth—*m.*	12.2	4.0	11.6	1.8	9.8	7.9	3.0	3.4	15.8	10.1

C.N.N. and the mesh depth ($r = 0.77$; $P = 0.01$). The relationship between catch and depth is summarized in the following tabulation:

Catch-per-net-night	*Standard position No. (and mean depth in* m.)
2.50 or greater	2 (4.0); 4 (1.8); 7 (3.0); 8 (3.4)
2.01–2.49	10 (10.1)
2.00 or less	1 (12.2); 3 (11.6); 5 (9.8); 6 (7.9); 9 (15.8) (mean depth all positions—11.5)

Only one fish was caught in a depth greater than the 15–20-m. zone, although altogether 55 sets were made in depths of 20–30 m. Fish of all nettable sizes were most abundant in shallow water down to depths of 10–15 m. Although the largest meshes, of No. 5 group, were set a total of 156 times, they took only one fish, and that in the 0–5-m. zone. The largest fish caught was taken by the No. 4 mesh group, at a depth of approximately 7 m.

(2) LAKELSE LAKE (Fig. 5)

Most of the fish were caught in very shallow water of 0–3 m.; and almost all within the depths of 0–6 m. A few fish were taken in depths of 6–12 m., but none at greater depths.

No fish larger than those taken in meshes of groups Nos. 1, 2 and 3 were caught. All meshes that did catch fish made their best catches in the 0–3-m. zone. The meshes of groups Nos. 1 and 2 caught fish in depths down to 6 and 9 m., respectively, but the larger meshes, of No. 3 group, took fish in only the 0–3-m. zone.

FOOD OF THE WHITEFISHES

MATERIALS AND METHODS

Stomachs of captured fish were severed at the oesophagus and pyloric sphincter. The contents were removed to Petri dishes, and were divided into the respective groups present. The numbers of organisms in each group were counted, and their volume determined by water displacement.

Methods commonly used to indicate the relative importance of specific organisms as food refer to the percentage by volume which they constitute of

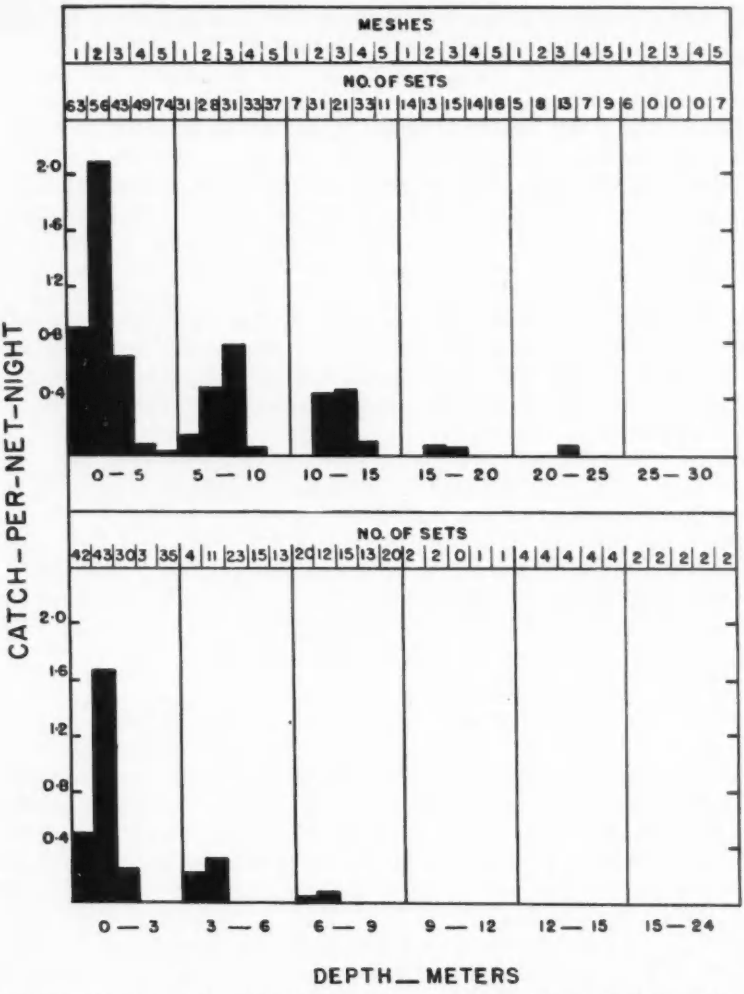

FIGURE 5. Catch-per-net-night of Rocky Mountain whitefish at different depths in Babine (A) and Lakelse (B) Lakes, 1946 and 1947.

the total food sample, or to the frequency of their occurrence among the fish in the sample. Either can often be misleading, or require qualification, for example, when a single or few fish have ingested a large volume of some food organism, or when all or many fish have each consumed very small amounts of some organism. To avoid too frequent qualifications, a simple consumption index (C.I.) is employed here which, as a unit, indicates the status of specific food items among each sample of stomach contents. It is the square root of the

product of the number of fish in the sample that have consumed the organism in question, and the average volume of that organism in the stomachs of all the fish in the sample. Thus, the magnitude of the C.I. indicates the relative importance of specific organisms as food, within specific samples (that is, their importance within the sample, by rank). Comparison between one sample and another can be made by comparing the ranks of particular C.I.'s.

All tables summarizing the stomach contents of fishes, both whitefish and other species, appear in the Appendix, and have numbers prefaced with "A".

COMMON WHITEFISH

(1) BABINE LAKE (Table A1).

Bottom organisms, such as larval insects and small molluscs, made up more than 80 per cent by volume of the stomach contents of the whole sample. Plankton crustacea, such as the copepod *Heterocope*, and the cladocerans *Bosmina* and *Daphnia* were occasionally important, apparently having been consumed in large numbers when encountered.

The small gastropods constituted the most important single item of food; almost 62 per cent of the fish had eaten these forms, and they made up 71 per cent of the total volume of food present.

The more important C.I.'s were: Gastropoda, 8.5; Trichoptera, 2.4; Copepoda, 1.6; combined Mollusca, 8.6; combined Insecta, 3.6; combined Crustacea, 1.9.

Gastropoda and the relatively large copepod, *Heterocope,* had been eaten mainly by larger fish. Chironomids and caddis larvae had been eaten by fish of all sizes, but the larger forms of caddis worms mostly by larger fish.

(2) MORRISON LAKE (Table A2)

The food of the common whitefish in Morrison Lake was strikingly different from that of the Babine fish. Almost 98 per cent of the Morrison Lake fish whose stomachs contained any food at all had eaten plankton crustaceans. Only 13 per cent of the fish had ingested small amounts of larval insects (mostly chironomids); and only 8 per cent had taken small numbers of molluscs.

The most frequently occurring crustacean was *Heterocope.* This organism alone constituted 86 per cent of the total volume of food consumed, and had been taken by 72 per cent of the fish.

The C.I. for *Heterocope* was 4.3, and for all crustaceans, 4.8.

ROCKY MOUNTAIN WHITEFISH

(1) BABINE LAKE (Tables A3, A4)

Insect young dominated the diet; they had been taken by more fish than had other organisms, and constituted the greatest percentage by volume. Of the 121 specimens, 72 per cent had eaten insects (almost entirely immature forms), 39 per cent had fed on small molluscs, and 17 per cent on plankton crustaceans.

The C.I.'s were: Insecta (immature), 11.0; Mollusca, 6.2; Crustacea, 1.6.

(2) LAKELSE LAKE (Tables A5, A7)

Immature aquatic insects were the most important items of diet. The remainder of the food was made up almost entirely of pelecypods and gastropods.

Aquatic insects, as nymphs and larvae, occurred in 80 per cent of the stomachs, and constituted 60 per cent of the diet by volume.

Among the Insecta, mayfly nymphs occurred most frequently, and also made up the greatest per cent volume, if allowance is made for the volume of the caddis larvae cases. The principal Ephemeridae were the burrowing type of the genus *Ephemera*.

Chironomids and caddis larvae constituted an approximately equal per cent volume, but the chironomids occurred in only 11 per cent of the stomachs, as compared with 42 per cent for the caddis larvae. Damselfly nymphs, adult aquatic beetles and other unidentified insect remains made up the remaining small amount of food.

The pelecypods were probably next in importance after mayfly nymphs, if allowance is again made for the volume of the caddis worm cases. However, in the large 1945 sample (Table A5) they occurred in only 11 per cent of the stomachs. Gastropods, the chief form of which was *Planorbis* (s.l.), were of relatively little importance.

The important C.I.'s were: Ephemerida, 3.4; Trichoptera (larvae and cases), 2.6; Pelecypoda, 1.7; Chironomidae (larvae), 1.3.

(3) MORRISON LAKE (Table A8)

Table A8 summarizes the contents of the nine specimens. The average volume of food per stomach was very low, the bulk of it being made up of aquatic insect material, and of immature insects in particular. Only one fish had taken a minute quantity of plankton crustaceans.

COMPETITORS FOR FOOD OF THE WHITEFISHES

METHODS AND MATERIALS

Similarities in their diet and in the habitat they occupy lead to competition for food between the whitefishes and other species. The important competitors for the food of the whitefishes have been assessed through the examination of many stomachs of several species of fish, and the determination of their habitats by an analysis of their depth distribution.

The depth distribution of the possible competitors has been determined in the same manner as for the whitefishes—by computing the C.N.N. in various depth zones. The data used were standard set catch records for 1946 and 1947. Where the total number of fish caught was small, the weighted mean depth of capture (from the records of both years) has been used. Some species are described as potential competitors on the basis of their stomach contents alone —these were the rarely caught fish.

PEAMOUTH CHUB (Tables A9, A10)

The food of the chub was very similar to that of both whitefishes, excepting that of the common whitefish in Morrison Lake. The bulk of the food of the three species consisted of such bottom forms as young aquatic insects and small molluscs. In Morrison Lake the diet of the relatively numerous common whitefish

was almost wholly plankton crustaceans; in contrast, very few peamouth chub and Rocky Mountain whitefish occur in Morrison Lake, and only small amounts of plankton material were found in the stomachs of samples of these fish.

The depth distribution of the peamouth chub in Lakelse Lake was very similar to that of the Rocky Mountain whitefish (compare Figures 5 and 6). Peaks of abundance for the two species were in the 0–5–m. zone.

Information on the depth distribution of the chub in Babine and Morrison Lakes is tabulated:

Lake	*No. captured*	*Weighted mean depth of capture*—m.
Babine (Div. I)	526	2.2
Babine (Wright Bay)	97	3
Morrison	50	3.9

These mean depths of capture of the peamouth chub are similar to the depths of maximum catches of Rocky Mountain whitefish in Babine Lake (Fig. 5). As in the case of the Rocky Mountain whitefish, however, the distribution of the chub also overlapped into the greater depths where common whitefish were most numerous (Fig. 4).

SQUAWFISH (Tables A11–A14)

Fishes (and some lampreys) made up most of the food eaten, but bottom organisms, including insect larvae and molluscs occasionally, were also important.

The C.N.N. of squawfish in Lakelse Lake is given in Figure 6. They were most abundant in the 0–5–m. zone, which was the region of maximum abundance of the Rocky Mountain whitefish (Fig. 5).

The depth distribution of the squawfish in Babine and Morrison Lakes is summarized below:

Lake	*No. captured*	*Weighted mean depth of capture*—m.
Babine (Div. I)	50	2.3
Babine (Wright Bay)	41	2.0
Morrison	83	3.4

They were caught most often in depths where both whitefishes, but especially the Rocky Mountain whitefish, were abundant (Fig. 4, 5).

CUTTHROAT TROUT (Tables A15–A20)

Although they had been mainly piscivorous, insect material made up approximately 40 per cent by volume of the food consumed (Babine and Lakelse samples). However, the greater part of the insect material consisted of terrestrial forms. In Lakelse Lake the trout had eaten mainly adult Coleoptera, whereas the Rocky Mountain whitefish had fed mostly on mayfly nymphs and caddis larvae. Molluscs were common in the whitefish food, but only two from among more than 500 trout had traces of molluscs in their stomachs. Similar differences between trout and Rocky Mountain whitefish were observed in Babine and Morrison Lakes.

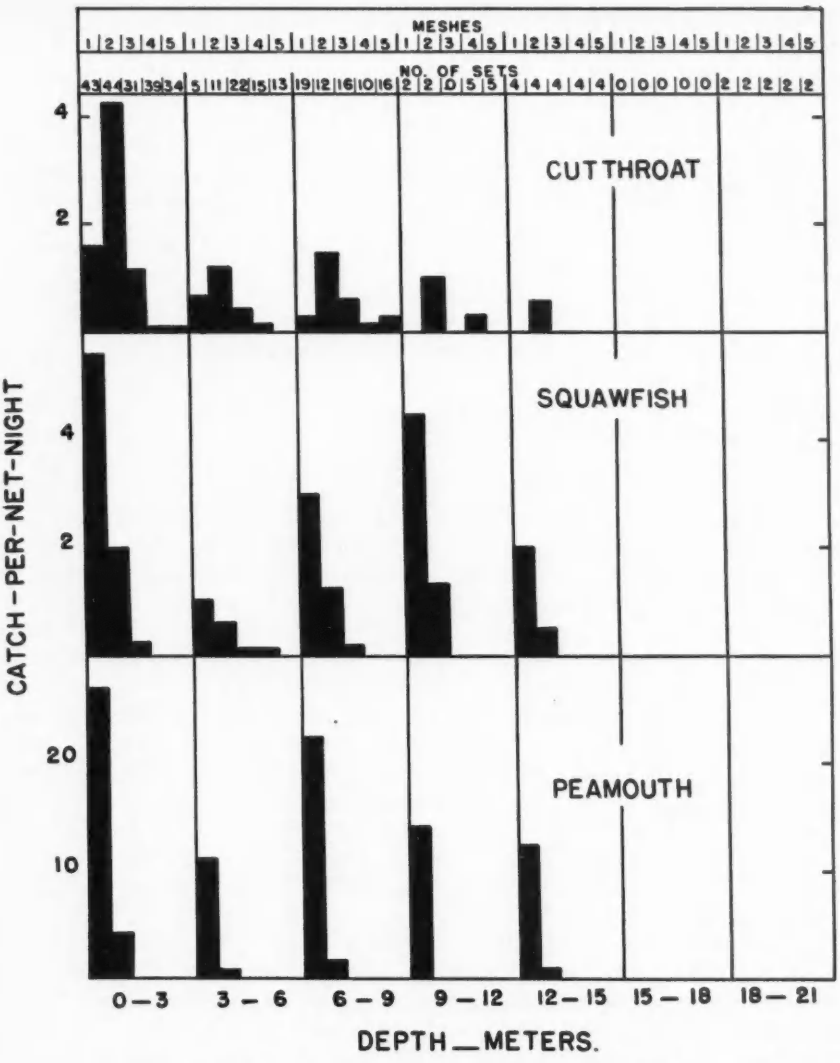

FIGURE 6. Catch-per-net-night of cutthroat trout, squawfish and peamouth chub at different depths in Lakelse Lake, 1946 and 1947.

The C.N.N. of cutthroat trout at different depths in Lakelse Lake is given in Figure 6. Standard sets made in deep water and laid along the bottom seldom caught these fish, although they were taken fairly frequently in the same waters by anglers. The largest net catches of trout of all sizes were in the shallow 0–5–m.

zone, so that it is evident that in summer months they do occur together with the Rocky Mountain whitefish.

Dolly Varden Char (Tables A21–A24)

Only a few char have been netted in Lakelse Lake and none in Babine or Morrison Lakes. The char had fed mostly upon small fishes, with only small quantities of bottom insect material or other organisms important in the whitefishes' diet.

Fine-scaled and White Suckers (Tables A25–A27)

Most of the food of both suckers consisted of larval insects, supplemented by small molluscs and plankton crustaceans. Their food was similar to that of both whitefishes, and they were taken most frequently in water shallower than 5 m. However, the numbers of these fish actually in the lakes during summer months are believed to be small (although they are often seen in adjacent streams).

PREDATORS OF THE WHITEFISH

Predators of the whitefish in three Skeena lakes have been identified by the contents of their stomachs. Although all the fish referred to below are piscivorous, and had whole or parts of fish in their stomachs, not all had remains that could be identified definitely as those of whitefish.

CUTTHROAT TROUT (Tables A15–A20). Fish were important in the cutthroats' diet but no whitefish remains were found in the Babine and Morrison samples, and no Rocky Mountain whitefish in the Lakelse samples.

SQUAWFISH (Tables A11–A14). No whitefish remains were identified in any of the samples from the three lakes, despite the abundance of these fish (particularly in Lakelse Lake) and the frequency of fishes in their diet. Stickleback, and young salmon and trout were the species found most often in squawfish stomachs.

DOLLY VARDEN CHAR (Tables A21–A24). Although all fish remains in Dolly Varden stomachs were identified to species, no Rocky Mountain whitefish remains were found.

LAKE TROUT (Tables A28–A29). In Babine Lake, among 53 specimens, 1 Rocky Mountain whitefish and 1 common whitefish were found in 2 stomachs. In addition, 4 other lake trout had remains of fish which were identified as either Coregonidae or Salmonidae (but not Oncorhynchus). In the 23 stomachs from Morrison Lake, 9 common whitefish and 1 Rocky Mountain whitefish had been taken by 4 trout; another trout had taken either Salmonidae or Coregonidae. Of the food consumed by the 23 Morrison Lake trout, common whitefish remains made up more than 50 per cent by volume.

RAINBOW TROUT. Only 6 specimens were available, all from Morrison Lake; 3 common whitefish had been taken by 1 trout.

LING (Tables A30–A31). No whitefish remains were identified in 12 Babine Lake specimens; among the 4 ling from Morrison Lake there were whitefish

remains in 2, and one other had taken either Salmonidae or Coregonidae. Ling are difficult to take in gill-nets, and are not captured in proportion to their probable abundance, as indicated by observations of many of these fish in shallow water during the time of the spring migrations of salmon smolts.

GROWTH OF THE WHITEFISHES

Materials and Methods

Age determinations were made from scales taken from whitefish of known fork length—59 common whitefish from Babine Lake, and 133 from Morrison Lake; 130 Rocky Mountain whitefish from Babine Lake, 118 from Lakelse Lake, and 11 from Morrison Lake. In comparing age with fork length, males and females have been grouped together.

Common Whitefish in Babine and Morrison Lakes.

Fork lengths at different ages are listed in Table XI. In their third year Babine fish were longer than Morrison fish, but from the third year on the increase in length with age was much the same for both groups.

No fish greater than 480 mm. fork length were netted in either lake. The oldest fish found in Babine Lake were 2 of X years of age, with a mean fork length of 473 mm.; and 2 of IX years of age, with a mean fork length of 441 mm., from Morrison Lake.

Table XI. Size of the common whitefish taken in Babine and Morrison Lakes.

Age in years completed	Mean fork length—*mm.*		No. of specimens	
	Babine	Morrison	Babine	Morrison
I	...	151	...	6
II	248	207	7	4
III	307	264	4	6
IV	365	307	8	5
V	384	321	11	15
VI	394	329	9	27
VII	419	344	10	29
VIII	449	366	7	2
IX	470	441	1	2
X	473	...	2	...

Rocky Mountain Whitefish in Babine and Lakelse Lakes

Growth data are summarized in Table XII. In their second year the Babine fish averaged a greater mean fork length than the Lakelse fish; from then on the increase in length with age was similar. Only 18 specimens were available from Morrison Lake.

The oldest fish taken were age IX fish from Lakelse (fork length 338 mm.) and Babine (fork length 365 mm.) Lakes; and several age VII fish from Morrison Lake (mean fork length 317 mm.).

TABLE XII. Size of the Rocky Mountain whitefish taken in Lakelse, Babine and Morrison Lakes.

Age in years completed	Mean fork length—*mm.*			No. of specimens		
	Lakelse	Babine	Morrison	Lakelse	Babine	Morrison
0	90	...	...	1	...	...
I	127	166	177	6	12	3
II	176	204	213	14	12	6
III	211	246	228	10	22	2
IV	242	366	...	31	26	...
V	281	281	...	28	17	...
VI	302	315	...	16	22	...
VII	336	341	317	7	16	7
VIII	330	348	...	4	9	...
IX	338	365	...	1	1	...

FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF SKEENA WHITEFISHES

COMMON WHITEFISH

Within the Skeena system the common whitefish has been taken in only Babine, Morrison, Bear and Azuklotz Lakes. These four lakes lie in the central plateau, east of the coastal range of mountains. They also have in common the fact that they are relatively deep and cold bodies of water, of the oligotrophic type. Other similar Skeena lakes have conditions that are probably unfavourable for the establishment of common whitefish populations, such as heavily glaciated waters, lack of shoals for spawning, and a poor abundance of food organisms (Morice, Kitsumgallum, Motase and Johnston, for example).

From a consideration of the distribution of the common whitefish throughout North America, it is apparent that it inhabits clear, cold and usually deep waters. In the large Canadian lakes where this fish is abundant enough to support commercial fishing, the supply of suitable food is much greater than in any of the Skeena lakes. Of particular importance as food for common whitefish in several of the large lakes is the amphipod *Pontoporeia* (Clemens *et al.*, 1924; Koelz, 1927; Rawson, 1947a.b; Larkin, 1948), which does not occur in the Skeena lakes.

There are no known physical barriers of recent origin which might have prevented the further distribution of the common whitefish in the Skeena system.

ROCKY MOUNTAIN WHITEFISH

The Rocky Mountain whitefish has been found in all the Skeena lakes where netting was done, and has been observed in many rivers and streams. This fish appears to be most abundant in eutrophic-type lakes, where there is at least a fairly good supply of bottom food organisms (Lakelse Lake, for example). Where the amount of bottom fauna was found to be sparse, as in Morrison Lake, there were very few Rocky Mountain whitefish.

The Rocky Mountain whitefish is believed to have repopulated British Columbia from a refuge centre south of the Pleistocene ice sheet (Carl and

Clemens, 1953). The Columbia and Fraser systems could have been the routes of its entry into the Skeena drainage.

SUMMARY

From data collected during 1944–1948 in the course of the Skeena River Salmon Investigation some features of the ecology of the common and Rocky Mountain whitefishes have been described.

The text contains a list of the Skeena lakes described in previous publications which, together with certain hitherto unpublished information, have been used to relate the known distribution of the two whitefishes in the Skeena system to the characteristics of its lakes.

Only four Skeena lakes are known to have populations of common whitefish. Other lakes were not examined adequately to be definite about their absence, but at the same time it is certain that they could not have been supporting large populations of common whitefish. All four lakes lie in the central plateau, west of the continental divide and east of the coastal range of mountains; and they also have in common characteristics that are mainly oligotrophic rather than eutrophic.

The Rocky Mountain whitefish has been found in all the Skeena lakes investigated, and these have varied from deep and cold bodies of water, to shallow and warm ponds. The species is probably most abundant in lakes of the eutrophic type.

From data collected more adequately in three lakes, the bottom faunas, the depth distribution of the two whitefishes, their food, and the fishes that compete for their food or predate on them have been described. These lakes are Babine (area, 445 sq. km., mean depth 49.1 m.); Morrison (area, 15 sq. km., mean depth 20.7 m.); and Lakelse (area, 14 sq. km., mean depth 7.3 m.).

A low abundance of bottom organisms was found in Babine Lake, roughly 175 organisms per sq. m., weighted for the area of different depth zones. A few dredge hauls made in Morrison Lake indicated that bottom fauna was even more sparse than in Babine Lake. In Lakelse Lake the estimated number of bottom organisms, weighted for areas of depth zones, was 628 per sq. m.

The summer depth distribution of the two species of whitefish was described from catch records of gill-netting by standardized procedures. Rocky Mountain whitefish were most abundant in shallow depths down to 5 m., and common whitefish in depths of 10–15 m. The distribution of the two species overlapped. Some differences in the distribution of small and large fish were described.

With the exception of the common whitefish in Morrison Lake, both species had fed almost wholly upon the bottom organisms present in the lake, and probably in proportion to the abundance of such organisms in the depth inhabited by the whitefish. In Morrison Lake more than 90 per cent by volume of the diet of common whitefish consisted of plankton crustaceans. This condition probably reflected the paucity of bottom organisms that occurs in that lake. Only a very small population of Rocky Mountain whitefish is present in Morrison Lake,

according to the gill-net catches. Samples of these had fed almost wholly on bottom organisms, and had taken very few plankters.

Competitors of the whitefish were assessed on the basis of a common diet and a common habitat. Peamouth chub were the most important competitors of the Rocky Mountain whitefish in Lakelse Lake, and of both species in Babine Lake. Very few chub were found in Morrison Lake, and these had consumed mostly bottom organisms. The depth distribution of the peamouth chub was very similar to that of the Rocky Mountain whitefish. Although squawfish were mainly piscivorous they had also consumed important amounts of bottom organisms. In summer they were taken most frequently in depths common to the Rocky Mountain whitefish. Cutthroat trout had eaten mostly small fish and terrestrial insects, but also quantities of bottom organisms. They were frequently captured in shallow water. The cutthroat trout and the squawfish occur in all three lakes. A few Dolly Varden char have been caught in Lakelse Lake, and their food was found to be mostly small fishes, with very little insect material. The fine-scaled sucker has been taken in the three lakes, and the white sucker in Babine and Morrison Lakes. Their food was quite similar to that of the whitefishes, but their relatively small numbers make them of no very great importance as competitors.

Predators of the whitefishes were determined upon the identification of whitefish remains in their stomachs. The most serious were the lake trout and the ling. Despite the frequency of a variety of fishes in their diet, other piscivorous fishes, such as squawfish, cutthroat trout and Dolly Varden char, had taken no identifiable whitefish. Common whitefish remains were found in the stomach of one rainbow trout in a small sample from Morrison Lake.

The growth of common whitefish in Babine and Morrison Lakes, and of Rocky Mountain whitefish in all three lakes, was determined from age readings from scales, and measurements of fork length. Because of more rapid growth in early years, Babine common whitefish between the ages of II and X years were larger than those of the same age in Morrison Lake; but the rate of growth in the later years was much the same for the two populations. In the case of Rocky Mountain whitefish in Babine and Lakelse Lakes the former grew more rapidly in early years, and later at a very similar rate to that of the Lakelse fish. Morrison Lake fish grew at a slower rate than Babine fish. The oldest fish found were X- and IX-year-old common whitefish in Babine and Morrison Lakes, respectively; IX-year-old Rocky Mountain whitefish in Babine and Lakelse Lakes, and VII-year-old Rocky Mountain whitefish in Morrison Lake.

From a consideration of the known distribution of the common whitefish in the Skeena lakes, and of the characteristics of the lakes in which they occur, it was suggested that their distribution is probably limited to relatively deep and cold lakes, and their abundance restricted by scarcity of suitable food. Organisms such as the amphipod *Pontoporeia*, which is so important a food item of the common whitefish in lakes where it is fished commercially, do not occur in anything approaching like abundance in the Skeena lakes. No known physical

barriers have prevented the further distribution of the common whitefish in the Skeena lakes.

The Rocky Mountain whitefish occurs in all the Skeena lakes that have been investigated. It appears to favour more productive lakes of the eutrophic type, and was scarce in Morrison Lake where the standing crop of bottom fauna was very small.

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APPENDIX

TABLES LISTING STOMACH CONTENTS, NUMBERS A1–A31

Explanations of terms used in these tables are as follows:

Occurrence	–	number of stomachs containing the organism
Frequency	–	total number of the organism in all the stomachs
Amount	–	total volume of the organism in all the stomachs, in cubic centimetres
Av. frequency	–	average number of the organism per stomach in the total sample
Av. amount	–	average volume of the organism per stomach in the total sample, in cubic centimetres
Volume	–	percentage by volume; volume of the organism expressed as a percentage of the total volume of food consumed by all the fish
C.I.		Consumption Index, see p. 517–518

Kinds of organisms listed are as follows unless otherwise noted:

Trichoptera	–	include larvae and cases
Ephemerida	–	nymphs
Coleoptera	–	adults
Plecoptera	–	nymphs
Odonata	–	nymphs
Hymenoptera	–	adults
Hemiptera	–	larvae
Neuroptera	–	adults
Lepidoptera	–	larvae
T	–	trace

All specimens were taken in gill-nets, unless otherwise noted. Their size was mostly in excess of 200 mm. (8 inches) fork length.

TABLE A1. Stomach contents of 39 common whitefish caught in Divisions I and II of Babine Lake, 1946 and 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Trichoptera	9	305	26.25	7.82	0.67	15.7	2.4
Diptera (chironomids)	7	137	0.63	3.51	0.02	0.4	0.3
Ephemerida	1	1	0.10	0.02	...	0.1	...
Amphipoda	2	4	T	0.10	T	T	...
Copepoda—*Heterocope*	7	...	13.10	...	0.34	7.9	1.5
Cladocera	4	...	1.30	...	0.03	0.8	0.4
Gastropoda	24	3,000	118.41	76.92	3.04	71.0	8.5
Pelecypoda	3	91	1.20	2.38	0.03	0.7	0.3
Cottus	1	2	1.50	0.05	0.04	0.9	0.2
Plant	19	...	3.82	...	0.10	2.3	1.4
Miscellaneous	...	...	0.50	...	0.01	0.3	...
Empty	2	...	...	...	...	...	...

TABLE A2. Stomach contents of 95 common whitefish caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Diptera (larvae)	12	52	0.19	0.55	...	0.63	0.2
Amphipoda—*Gammarus*	1	1	T	0.01	T	T	...
Copepoda—*Heterocope*	68	13,200	25.92	138.95	0.27	85.85	4.3
—*Diaptomus*	1	50	0.11	0.53	...	0.31	...
Cladocera—*Daphnia*	28	4,400	1.38	46.31	0.01	4.40	0.6
—*Bosmina*	16	1,700	0.45	17.89	0.01	1.57	0.3
Hydracarina	2	3	0.02	0.03	T	T	...
Pelecypoda	5	30	1.36	0.32	0.01	4.40	0.3
Gastropoda	3	5	0.06	0.05	T	T	...
Plant	...	...	0.90	...	0.01	2.83	...
Empty	12	...	...	...	...	...	...

TABLE A3. Stomach contents of 76 Rocky Mountain whitefish caught in Division II of Babine Lake, 1946 and 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Trichoptera	41	1,250	34.72	16.4	0.46	33.34	4.3
Coleoptera	6	9	0.16	0.1	...	0.15	0.1
Diptera[a]	21	1,236	7.25	16.3	0.10	6.96	1.4
Plecoptera	2	5	0.15	0.1	...	0.14	...
Ephemerida	14	246	5.96	3.2	0.08	5.72	1.0
Insect remains	...	...	0.57	...	0.01	0.55	...
Amphipoda	2	46	0.35	0.6	0.01	0.34	0.1
Cladocera[b]	12	20,000	3.30	263.2	0.04	3.17	0.7
Copepoda—*Heterocope*	13	1,000	1.10	13.2	0.01	1.06	0.4
Gastropoda	26	1,800	28.35	23.7	0.37	27.22	3.1
Pelecypoda	7	1,200	13.64	15.8	0.18	13.10	1.1
Plant	...	...	7.33	...	0.10	7.04	...
Miscellaneous	...	...	1.27	...	0.02	1.22	...
Empty	4	...	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.
[b]*Daphnia* and *Bosmina*.

TABLE A4. Stomach contents of 45 Rocky Mountain whitefish caught in Divisions I and III of Babine Lake, 1946 and 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Trichoptera	25	161	12.8	3.6	0.28	55.2	2.6
Ephemerida	3	21	0.2	0.5	...	0.9	...
Plecoptera	2	42	0.7	0.9	0.02	3.0	0.2
Odonata	1	3	0.8	0.1	0.02	3.4	0.2
Diptera	14	121	1.3	2.7	0.03	5.6	0.7
Hydracarina	3	32	0.1	7.1	...	0.4	...
Gastropoda	11	192	6.1	4.3	0.14	26.3	1.2
Pelecypoda	1	6	0.1	0.1	...	0.4	...
Copepoda—*Heterocope*	2	...	0.4	...	0.01	1.7	0.2
Cladocera—*Bosmina*	5	...	0.2	...	...	0.9	...
Plant	6	...	0.5	...	0.01	2.1	0.2
Empty	12	...	...	...	...	...	...

TABLE A5. Stomach contents of 62 Rocky Mountain whitefish caught in Lakelse Lake, 1945.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			c.c.		*c.c.*	%	
Ephemerida	35	319	20.90	8.15	0.34	23.95	3.4
Odonata	3	3	0.35	0.48	0.01	0.40	...
Trichoptera	26	306	16.81	4.94	0.27	19.26	2.6
Diptera[a]	7	2,832	12.90	46.68	0.21	14.78	1.2
Coleoptera	2	2	0.02	0.03	T	T	...
Insect remains	...	...	0.60	...	0.01	0.69	...
Gastropoda	8	115	3.89	1.86	0.06	4.46	0.7
Pelecypoda	7	598	25.80	9.65	0.42	29.57	1.7
Amphipoda—*Hyalella*	3	126	0.30	2.03	0.01	0.34	...
Fish eggs	1	...	1.00	...	0.02	1.15	...
Miscellaneous	...	...	0.02	...	T	T	...
Plants	12	...	4.67	...	0.08	5.35	...
Empty	1	...	...	...	...	...	...

[a]Chironomid pupae and larvae.

TABLE A6. Stomach contents of 15 Rocky Mountain whitefish caught in Lakelse Lake, 1946.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Ephemerida	6	56	2.72	3.73	0.18	10.19
Trichoptera	7	270	15.00	18.00	1.00	56.24
Odonata	2	20	1.10	1.33	0.07	4.12
Insect remains	1	...	0.05	...	...	0.19
Gastropoda	2	51	2.00	3.40	0.13	7.49
Pelecypoda	3	110	5.60	7.33	0.37	20.99
Plant	1	...	0.20	...	0.01	0.75
Empty	1	...	...	...	...	...

TABLE A7. Stomach contents of 7 Rocky Mountain whitefish caught in Lakelse Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Ephemerida	3	17	0.74	2.43	0.21	4.82
Trichoptera	2	21	0.80	3.00	0.11	5.22
Diptera[a]	2	850	2.90	121.43	0.41	18.90
Gastropoda	1	1	T	0.14	T	...
Pelecypoda	2	140	9.40	20.00	1.20	61.27
Plant	1	...	1.50	...	0.21	9.78
Empty	0	...	...	...	...	...

[a]Chironomid larvae.

TABLE A8. Stomach contents of 9 Rocky Mountain whitefish caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Ephemerida	3	...	1.70	...	0.19	23.0
Trichoptera	5	60	4.80	6.6	0.53	64.9
Plecoptera	1	1	0.10	...	0.01	1.3
Odonata	1	1	0.08	...	0.01	1.1
Diptera[a]	2	11	0.22	1.2	0.02	3.0
Cladocera	1	20	T	2.2	...	...
Gastropoda	1	5	T	0.6	...	...
Plant	...	...	0.50	...	0.06	6.8
Empty	1	...	...	...	...	...

[a]Chironomid adults.

TABLE A9. Stomach contents of 31 peamouth chub caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Trichoptera	11	149	2.55	4.80	0.08	15.1	1.0
Coleoptera	1	1	T	0.03	...	...	...
Diptera[a]	5	94	0.10	3.03	...	0.5	0.2
Insect remains	6	...	0.10	...	...	0.5	0.2
Amphipoda	7	38	0.15	1.22	0.01	0.9	0.2
Cladocera	1	1	T	0.03	...	...	...
Hydracarina	1	1	T	0.03	...	...	...
Gastropoda	19	...	13.95	...	0.45	82.5	2.0
Bryozoa	1	1	0.10	0.03	...	0.5	...
Empty	3	...	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.

TABLE A10. Stomach contents of 41 peamouth chub caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	10	30	0.46	0.73	0.01	8.59	0.3
Plecoptera	1	4	T	0.08	...	...	...
Trichoptera	16	71	1.54	1.77	0.04	28.90	0.8
Diptera (larvae)	10	132	0.10	3.22	...	1.56	0.2
Coleoptera	5	15	0.20	0.37	0.01	3.91	0.2
Hymenoptera	1	1	T	0.02	...	...	...
Insect remains	8	...	0.40	...	0.01	7.03	0.3
Amphipoda—*Hyalella*	2	13	0.40	0.32	0.01	7.03	0.2
Gammarus	1	4	T	0.09	...	...	...
Cladocera—*Daphnia*	1	20	T	0.49	...	...	...
Hydracarina	1	1	T	0.02	...	...	...
Gastropoda	13	32	2.10	0.78	0.05	39.84	0.8
Plant	6	...	0.18	...	...	3.12	0.2
Empty	9	...	...	...	...	...	...

TABLE A11. Stomach contents of 202 squawfish caught in Lakelse Lake, 1945.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	7	85	3.80	0.42	0.02	2.16	0.3
Trichoptera	4	8	2.50	0.04	0.01	1.36	0.2
Diptera (adults)	2	1	T	0.01	...	...	...
Coleoptera	2	...	0.10	...	...	...	...
Hymenoptera	1	...	0.40	...	...	0.23	...
Insect remains	..	...	3.55	...	0.02	2.04	...
Gastropoda	2	5	4.10	0.03	0.02	2.27	0.2
Mollusc remains	1	...	0.20	...	...	0.11	...
Sockeye salmon	7	22	25.80	0.11	0.13	14.55	1.0
Salmonidae	11	16	12.80	0.08	0.06	7.16	0.8
Stickleback	37	53	27.49	0.26	0.14	15.45	2.2
Cottus	6	7	47.00	0.04	0.23	26.48	1.2
Peamouth chub	1	1	29.00	0.01	0.14	16.36	0.4
Fish remains	21	16	7.50	0.08	0.04	4.20	0.9
Fish eggs	6	...	6.50	...	0.03	3.64	0.4
Lamprey	10	9	4.65	0.05	0.02	2.61	0.5
Miscellaneous	...	...	1.25	...	0.01	0.68	...
Plant	6	...	1.20	...	0.01	0.68	0.2
Empty	69	...	...	...	...	...	...

TABLE A12. Stomach contents of 209 squawfish caught in Lakelse Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	10	11	1.08	0.05	0.01	1.99	0.2
Odonata	1	3	0.10	0.01	...	0.18	...
Plecoptera	3	5	0.87	0.02	...	1.60	0.1
Trichoptera	8	18	2.80	0.09	0.01	5.16	0.3
Hemiptera	2	250	4.20	...	0.02	7.74	0.2
Coleoptera	2	2	0.07	0.01	...	0.13	...
Insect remains	...	...	3.28	...	0.02	6.04	0.8
Lamprey	3	2	3.02	0.01	0.01	5.56	0.2
Sockeye salmon	5	11	10.30	0.05	0.05	18.97	0.5
Salmonidae	8	8	3.86	0.04	0.02	7.12	0.4
Peamouth chub	1	1	5.20	0.01	0.03	9.58	0.2
Stickleback	12	12	5.37	0.06	0.03	9.89	0.6
Fish remains	48	...	10.57	...	0.05	19.47	1.5
Fish eggs	7	...	1.90	...	0.01	3.50	0.3
Plant	9	...	1.50	...	0.01	2.76	0.3
Miscellaneous	1	...	0.18	...	...	0.33	...
Empty	74	...	...	...	...	...	...

TABLE A13. Stomach contents of 14 squawfish caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Trichoptera—larvae	1	5	0.2	0.36	0.01	2.5
—cases	1	3	0.4	0.21	0.03	7.5
Insects remains	3	...	2.0	...	0.14	35.0
Fish remains	2	2	1.0	0.14	0.07	17.5
Gastropoda	1	5	1.8	0.36	0.13	32.5
Amphipoda—*Hyalella*	1	1	T	0.07	...	...
Plant	1	...	0.3	...	0.02	5.0
Empty	10	...	...	...	...	...

TABLE A14. Stomach contents of 45 squawfish caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	6	18	0.60	0.40	0.01	2.57	0.3
Trichoptera	18	112	4.20	2.49	0.09	18.38	1.3
Coleoptera	1	1	T	0.02	...	...	...
Diptera[a]	2	4	0.05	0.08	...	0.20	...
Insect remains	9	...	0.80	...	0.02	3.58	0.4
Amphipoda	1	1	T	0.02	...	...	...
Gastropoda	5	7	2.6	0.15	0.06	11.46	0.5
Salmonidae or Coregonidae	1	1	T	0.02	...	...	...
Cyprinidae	2	2	0.85	0.04	0.02	3.75	0.2
Cottus	4	4	3.55	0.08	0.08	15.61	0.6
Fish remains	3	3	0.25	0.06	0.01	0.99	0.2
Bryozoa	1	...	0.05	0.22	...	0.20	...
Plant	3	...	0.20	...	...	0.79	0.1
Frog	1	1	9.70	0.02	0.22	42.49	0.5
Empty	3	...	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.

TABLE A15. Stomach contents of 141 cutthroat trout caught in Lakelse Lake, 1945.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	28	973	36.87	6.90	0.26	14.2	2.6
Odonata	13	16	3.08	0.11	0.02	1.1	0.5
Plecoptera (adults)	3	10	0.10	0.07	...	...	...
Trichoptera	22	77	9.27	0.55	0.07	3.8	1.2
Hemiptera	5	4	0.23	0.02	...	...	...
Diptera	4	8	0.50	0.06	...	...	...
Coleoptera	45	1,000	41.90	7.09	0.30	16.3	3.7
Hymenoptera	18	79	5.35	0.56	0.04	2.2	0.8
Insect remains	...	...	6.50	...	0.05	2.7	...
Arachnida	4	4	0.20	0.03	...	...	...
Amphipoda	2	...	T	...	...	...	...
Phyllopoda	1	3	0.20	0.20	...	...	...
Mysis	5	92	1.80	0.65	0.01	0.5	0.2
Gastropoda	1	2	0.05	0.01	...	...	...
Sockeye salmon	15	51	46.13	0.36	0.33	17.9	2.2
Pink salmon	1	25	4.20	0.18	0.03	1.6	0.2
Salmonidae	3	15	4.50	0.11	0.03	1.6	0.3
Stickleback	54	283	81.72	2.01	0.58	31.5	5.6
Cottus	1	1	9.50	0.01	0.07	3.8	0.3
Fish remains	9	10	3.60	0.07	0.03	1.6	0.5
Plant	7	...	3.45	...	0.02	1.1	0.4
Miscellaneous	1	...	0.60	...	...	...	...
Empty	10	...	...	...	...	...	...

TABLE A16. Stomach contents of 276 cutthroat trout caught in Lakelse Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	55	839	37.67	3.04	0.14	9.01	2.7
Odonata	12	20	1.07	0.07	...	0.26	0.2
Plecoptera	36	286	32.47	1.04	0.12	7.77	2.1
Trichoptera	34	99	15.53	0.36	0.06	3.72	1.4
Hemiptera (adults)	1	2	0.05	0.01	...	0.01	...
Diptera (adults)	13	96	4.22	0.35	0.02	1.01	0.4
Coleoptera	110	1,373	55.18	4.98	0.20	13.20	4.7
Hymenoptera	20	176	11.84	0.64	0.04	2.83	0.9
Neuroptera	4	180	3.10	0.65	0.01	0.74	0.2
Lepidoptera	1	1	0.30	...	...	0.07	...
Insect remains	...	...	19.59	...	0.07	4.69	...
Arachnida	1	2	0.02	0.01	...	0.01	...
Amphipoda	1	1	T	...	...	...	...
Mysis	...	44	1.19	0.16	...	0.29	...
Sockeye salmon	35	154	75.38	0.56	0.27	18.04	3.1
Cutthroat trout	1	3	20.00	0.01	0.07	4.79	0.3
Salmonidae	6	7	12.75	0.03	0.05	3.05	0.5
Stickleback	66	349	102.07	1.26	0.37	24.42	4.9
Cottus	1	1	5.00	...	0.02	1.20	0.2
Fish remains	36	...	10.67	...	0.04	2.55	1.2
Hirudinea	1	1	0.30	...	...	0.07	...
Porifera	4	...	2.92	...	0.01	0.70	...
Plant	17	...	6.52	...	0.02	1.56	0.7
Miscellaneous	...	...	0.10	...	...	0.02	...
Empty	13	...	...	...	...	...	...

TABLE A17. Stomach contents of 15 cutthroat trout caught in Lakelse River, 1945. Taken by hand-seine, hook and line.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Ephemerida	1	50	2.60	3.33	0.17	19.1
Odonata	3	3	0.15	0.20	0.01	1.1
Plecoptera	2	2	0.22	0.13	0.02	1.7
Trichoptera	2	18	1.00	1.20	0.67	7.4
Diptera	1	3	0.10	0.20	0.01	0.8
Coleoptera	5	103	2.67	6.87	0.18	19.6
Hymenoptera	2	6	0.05	0.40	...	0.3
Insect remains	...	...	0.44	...	0.03	3.2
Arachnida	1	1	0.05	0.07	...	0.3
Sockeye salmon	1	1	2.60	0.07	0.17	19.1
Stickleback	2	2	2.00	0.13	0.13	14.6
Fish remains	1	1	0.30	0.07	0.02	2.2
Plant	3	...	1.44	...	0.10	10.8
Empty	3	...	...	...	...	...

TABLE A18. Stomach contents of 69 cutthroat trout caught in Lakelse Lake, 1948. Taken by angling.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	7	21	0.80	0.30	0.01	1.31	0.3
Coleoptera	21	219	12.80	3.17	0.19	21.02	2.0
Odonata	6	10	0.55	0.14	...	0.90	0.2
Trichoptera	8	19	2.45	0.28	0.04	4.02	0.5
Hemiptera	2	16	0.39	0.23	0.01	0.64	0.1
Plecoptera	1	1	0.10	0.01	...	0.16	...
Diptera (adults)	1	6	0.20	0.09	...	0.33	...
Insect remains	...	...	3.05	...	0.04	5.01	...
Gastropoda	1	20	2.00	0.28	0.03	3.28	0.2
Amphipoda	1	2	0.02	0.03	...	0.03	...
Sockeye salmon	1	2	1.20	0.03	0.02	1.97	0.2
Salmonidae	2	5	3.88	0.07	0.06	6.37	0.3
Cyprinidae	1	1	3.70	0.01	0.05	6.08	0.2
Stickleback	13	35	15.75	0.51	0.23	25.86	1.7
Fish remains	5	5	12.55	0.07	0.18	20.61	1.0
Plant	6	...	1.35	...	0.02	2.22	0.3
Empty	15	...	...	...	...	...	...

TABLE A19. Stomach contents of 14 cutthroat trout caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Ephemerida	6	38	3.0	2.7	0.21	4.0
Trichoptera	7	48	6.1	3.4	0.43	8.4
Coleoptera	9	80	1.8	0.6	0.13	2.6
Hemiptera	2	7	0.2	0.5	0.01	0.2
Lepidoptera	2	3	0.4	0.2	0.03	0.6
Orthoptera	1	3	1.5	0.2	0.11	2.1
Hymenoptera	5	144	12.9	10.3	0.92	17.9
Diptera[a]	2	9	0.1	0.6	...	...
Insect remains	7	...	8.6	...	0.61	11.9
Nymphal cases[b]	3	6	2.5	0.4	0.18	3.5
Peamouth chub	1	1	21.0	0.1	1.50	29.2
Cyprinidae	1	10	5.0	0.7	0.36	7.1
Sucker	1	2	9.0	0.1	0.64	12.6
Hyalella	1	2	T	0.1	...	...
Empty	0	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.
[b]Ephemerida.

TABLE A20. Stomach contents of 3 cutthroat trout caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Trichoptera (pupa)	1	1	T	0.33	...	...
Coleoptera	1	3	0.1	1.00	0.03	33.3
Fish remains	1	1	0.2	0.33	0.06	66.6
Empty	1	...	...	...	...	...

TABLE A21. Stomach contents of 7 Dolly Varden char caught in Lakelse Lake, 1945.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Trichoptera	1	2	T	0.29	...	...
Salmonidae	2	2	2.30	0.29	0.33	20.00
Fish remains	1	2	9.00	0.29	1.29	78.18
Plant	...	...	0.18	...	0.03	1.82
Empty	3	...	...	...	...	...

TABLE A22. Stomach contents of 9 Dolly Varden char caught in Lakelse Lake, 1946. Taken by angling.

Organisms	Occurrence	Frequency	Amount
			cc.
Coleoptera	1	4	0.15
Sockeye salmon	1	1	2.00
Cottus	2	2	27.10
Sucker	1	1	48.00
Fish remains	2	2	0.65
Empty	2	...	...

TABLE A23. Stomach contents of 12 Dolly Varden char caught at Lakelse Lake, 1947. Taken in the yearling sockeye trap in the Lakelse River.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Odonata	1	5	0.40	0.42	0.03	0.71
Trichoptera	1	1	0.20	0.08	0.02	0.35
Insect remains	...	...	0.05	...	...	0.01
Cottus	1	1	56.00	0.08	4.67	98.86
Empty	9	...	...	...	...	...

TABLE A24. Stomach contents of 13 Dolly Varden char caught in Lakelse Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Coleoptera	1	1	0.02	0.08	...	0.28
Trichoptera	2	3	0.25	0.23	0.02	3.56
Sockeye salmon	1	2	0.55	0.15	0.04	7.82
Coho salmon	1	1	6.00	0.08	0.46	85.47
Plant	1	...	0.20	...	0.15	2.85
Empty	8	...	...	...	...	...

TABLE A25. Stomach contents of 3 white suckers caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount
			cc.
Ephemerida	2	16	5.3
Trichoptera	2	22	7.3
Diptera[a]	3	Many	...
Amphipoda—*Gammarus*	1	2	0.6
—*Hyalella*	3	65	21.6
Hydracarina	1	3	1.0
Gastropoda	2	6	2.0
Pelecypoda	2	7	2.3
Cladocera—*Bosmina*	1	T	T
Miscellaneous[b]	...	...	...
Empty	0	...	...

[a]Mostly chironomid pupae and larvae.

[b]Including various diatoms, filamentous algae, and *Vorticella*.

TABLE A26. Stomach contents of 6 fine-scaled suckers caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount
			cc.
Ephemerida	2	16	2.6
Trichoptera	4	60	10.0
Coleoptera	2	2	0.3
Diptera[a]	4	51	8.5
Amphipoda—*Hyalella*	3	84	14.0
Species	1	5	0.8
Ostracoda	2	10	1.6
Hydracarina	2	...	...
Gastropoda	2	6	1.0
Pelecypoda	1	1	0.2
Copepoda—*Cyclops*	1	...	...
Cladocera—*Bosmina*	2	...	...
Plant	2	...	...
Empty	1	...	...

[a]Mostly chironomid pupae and larvae.

TABLE A27. Stomach contents of 4 fine-scaled suckers caught in Morrison Lake, 1947.

Organisms	Occurrence	Relative abundance
Diptera (larvae)	4	Large numbers
Cladocera—*Daphnia*	1	Trace
—*Bosmina*	1	Trace
Copepoda—*Cyclops*	2	Trace
Ostracoda	3	Small numbers
Pelecypoda	1	Small numbers
Mollusc remains	2	Trace
Plant	3	Small amount
Empty	0	...

TABLE A28. Stomach contents of 53 lake trout caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	7	15	0.35	0.28	0.01	0.1	0.2
Trichoptera	3	35	1.90	0.66	0.04	0.7	0.3
Coleoptera	2	2	0.08	0.04	...	...	...
Lepidoptera	1	1	0.20	0.02	...	0.1	...
Diptera[a]	14	49	0.50	0.94	0.01	0.2	0.4
Diptera (adult)	2	3	T	0.06	...	...	...
Insect remains	3	...	T	...	...	...	...
Sockeye salmon	2	3	1.70	0.06	0.03	0.7	0.2
Kokanee (adult)	1	1	105.00	0.02	1.98	40.6	1.4
Coho salmon	1	2	6.80	0.04	0.13	2.7	0.4
Salmonidae	5	4	1.10	0.08	0.02	0.4	0.3
Salmonidae or Coregonidae	4	7	12.00	0.13	0.23	4.6	1.0
Coregonidae	2	2	29.60	0.04	0.56	11.4	1.0
Ling	1	1	33.00	0.02	0.62	12.8	0.8
Cottus	2	2	14.70	0.04	0.28	5.7	0.7
Fish remains	12	12	46.95	0.23	0.89	18.2	3.3
Amphipoda—*Gammarus*	1	1	0.05	0.02	...	...	...
Copepoda—*Heterocope*	6	...	0.60	...	0.01	0.2	0.3
Porifera	4	...	2.50	...	0.05	0.9	0.4
Plant	3	...	1.70	...	0.03	0.7	0.3
Empty	21	...	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.

TABLE A29. Stomach contents of 23 lake trout caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume	C.I.
			cc.		*cc.*	%	
Ephemerida	1	2	0.1	...	...	0.04	...
Diptera[a]	2	11	T	0.48	...	...	...
Insect remains	3	4	0.1	0.18	...	0.04	0.1
Kokanee	2	2	82.0	0.09	3.56	33.43	2.6
Coregonidae	4	10	129.5	0.43	5.63	52.87	4.7
Salmonidae or Coregonidae	1	1	0.6	0.04	0.03	0.24	0.2
Peamouth chub	1	1	3.1	0.04	0.14	1.27	0.4
Redside shiner	1	2	4.7	0.09	0.20	1.92	0.4
Cottus	2	2	6.0	0.09	0.26	2.44	0.7
Fish remains	6	9	13.0	0.39	0.57	5.31	1.8
Copepoda—*Heterocope*	2	8	T	0.35	...	...	...
Clodocera—*Bosmina*	2	1	T	0.04	...	...	...
Porifera	7	...	6.0	...	0.26	2.44	1.3
Empty	7	...	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.

TABLE A30. Stomach contents of 12 ling caught in Babine Lake, 1946.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Ephemerida	1	1	T	0.08	...	...
Trichoptera	2	2	0.25	0.17	0.02	3.3
Diptera[a]	1	1	T	0.08	T	...
Insect remains	2	...	T	...	...	...
Cottus	1	1	1.6	0.08	0.13	20.6
Cyprinidae	1	1	0.4	0.08	0.03	5.1
Fish remains	3	5	0.9	0.42	0.08	0.6
Amphipoda—*Hyalella*	1	1	0.1	0.08	...	0.6
Copepoda—*Heterocope*	2	4	T	0.32	...	...
Chilopoda (centipede)	1	1	0.1	0.08	...	0.6
Hirudinea	1	6	4.50	0.50	0.38	53.1
Empty	4	...	...	...	...	...

[a]Mostly chironomid pupae and larvae.

TABLE A31. Stomach contents of 4 ling caught in Morrison Lake, 1947.

Organisms	Occurrence	Frequency	Amount	Average frequency	Average amount	Volume
			cc.		*cc.*	%
Whitefish	2	3	17.3	0.75	4.33	17.03
Salmonidae or Coregonidae	1	1	0.3	0.25	0.01	0.02
Peamouth chub	1	1	84.3	0.25	21.08	82.94
Empty	1	...	...	...	...	...

The Standing Crop of Fish in Lakes[1,2,3]

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ABSTRACT

To determine whether certain environmental factors may affect standing crop, an analysis was made, primarily by regression methods, of the published estimates of standing crops of fish in lakes and ponds. Standing crop estimates derived by draining and those by poisoning appear to be equally accurate, but marking and recovery estimates may not be directly comparable with the other two. Average standing crops in river backwaters and oxbows were almost 500 pounds per acre; in midwestern reservoirs, almost 400 pounds per acre; in other reservoirs and ponds, 200 to 300; in warm-water lakes, 125 to 150; and in trout lakes, less than 50 pounds per acre.

No correlation could be shown between areas of lakes or ponds and their standing crops per acre. There was a tendency for standing crop per acre to decrease with increase in maximum depth of trout lakes, of warm-water lakes, and probably of reservoirs. Significant increase in standing crop per acre with increase in carbonate content of the water was found in trout lakes, warm-water lakes and midwestern reservoirs.

Elton's pyramid of numbers was demonstrated in an analysis of standing crop per acre by species. Competition between species at the same food level may be mitigated by habitat segregation. Standing crop per acre increases as the number of species increases or as the niches are filled. However, standing crops of given species were usually highest when only one or two species were present. Regressions of the standing crops of one species upon those of other species may give clues as to the degree of competition or of protocooperation, but these clues must be critically evaluated since the regressions may be due to factors other than the presence of the other species.

INTRODUCTION

In recent years, the standing crop of fish has been determined for a number of lakes and ponds by draining the body of water, by killing the fish with copper sulphate or rotenone, by marking and recovery population estimates or by intensive netting. This paper summarizes the published data, attempts to derive standards which may be used for comparative purposes and investigates the relationships between standing crop and some environmental factors. Standing crops of fish do not necessarily bear a close relationship to fish production [49], but usually the standing crop is the only available estimate of fish production. Since the annual rate of turnover probably varies less from one fish population to another than does the standing crop, standing crop data are probably fairly good estimates of fish production.

[1]Received for publication January 4, 1955.

[2]From the Iowa Cooperative Fisheries Research Unit, sponsored by Iowa State Conservation Commission and the Industrial Science Research Institute of Iowa State College.

[3]A paper presented at the 8th meeting of the Canadian Committee for Freshwater Fisheries Research, held at Ottawa, January 3, 1955.

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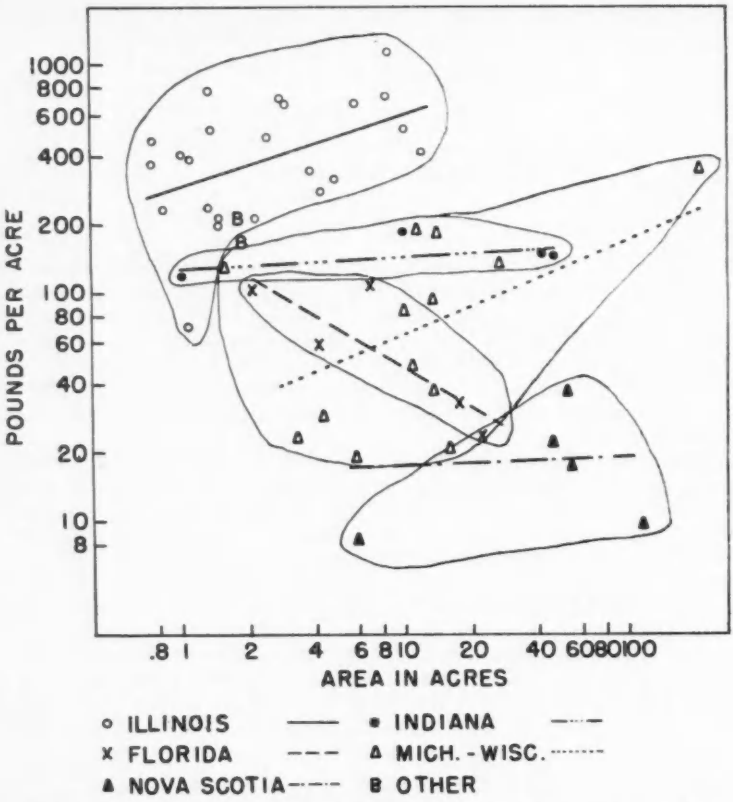

FIGURE 1. Regressions of logarithm of standing fish crop upon logarithm of area, for five groups of lakes studied by Rounsefell [52].

Rounsefell [52] demonstrated a negative regression of standing crop and annual yield upon the area of the lake. The larger the lake the smaller the standing crop per acre, and the smaller the annual yield per acre. A re-check of the data indicates that the relationship is not as clearly defined as Rounsefell suggested. Most of the lakes over 40 acres for which Rounsefell had standing crop estimates were trout lakes in Nova Scotia, and most of the lakes under 4 acres were warm-water ponds in Illinois. His data may be readily separated into five lake types as follows (see also Fig. 1):

Twenty-two Illinois reservoirs, which were drained or poisoned, ranging from 0.75 to 12.1 acres in area, and having from 71 to 1,145 pounds of fish per acre. The regression line for these data is:

$$P = 2.154 + 0.3155\,A$$

where P is the logarithm of the standing crop in pounds per acre
and A is the logarithm of the area in tenth acres.

Four Indiana lakes, where the population was estimated by marking and recovery, from 1 to 47 acres in area, and having 117 to 186 pounds of fish per acre, with a regression line of:

$$P = 2.057 + 0.0532\ A.$$

Thirteen Michigan and Wisconsin lakes, mostly poisoned to reclaim for trout, 1.6 to 200 acres in area, with standing crops of 21 to 357 pounds per acre, and a regression line of:

$$P = 0.990 + 0.4184\ A.$$

Five Florida lakes, treated with rotenone, 2.1 to 24 acres, with 22.2 to 105.0 pounds per acre, and a regression line of:

$$P = 2.853 - 0.5911\ A.$$

Five Nova Scotia trout lakes, 6 to 113 acres, with 9.7 to 36.0 pounds per acre, and a regression of:

$$P = 1.148 + 0.0197\ A.$$

Since four of the five regressions are positive rather than negative, there is obviously no general tendency for crop per unit area to decrease with size, within these groupings. Two Alabama ponds of 1.78 to 1.8 acres are not included in the above groups, but their values could have been included with the Indiana or the Illinois lakes with little effect on the regressions.

As regards the yields per acre, the regressions which Rounsefell reported may be a function of the fishing effort per acre, rather than actual fish production as he implied. There is no exact information on relative effort (per acre) employed on the lakes he used, but in general it could be expected to decrease with size.

RELATION OF STANDING CROP OF FISH TO AREA

Now that data on many more lakes are available it may be well to re-evaluate the relationship between standing crop per acre and area of the lake, to see if a real effect may not exist after all. A decrease in fish production with increase in area is a relationship which has logical basis in several limnological concepts of lake productivity (see particularly Rawson [44]).

First, I wish to point out that the available data are probably not very typical of lakes in general. Most of the standing crop estimates have been made on small ponds which have been stocked with a limited number of species of fish or have been on lakes which had populations which were undesirable.

Prior to analysis, the data were separated into groups according to the methods whereby the population estimates were made and according to lake type, in so far as this was possible from the published information (Tables I, II). The population estimates made by draining some reservoirs in the midwestern states were found to be similar to estimates made by poisoning other reservoirs (Fig. 2, Table III). Likewise, the marking and recovery estimates on a series of midwestern warm-water lakes did not seem to be significantly different from the estimates from poisoning a series of somewhat similar lakes (an F of 0.1, with 1 and 20 degrees of freedom) (Table II, groups C, D). Marking and recovery

TABLE 1. Standing crops of fish in United States reservoirs, in relation to area. (Significance of regression coefficients or F-values in this and subsequent tables is indicated as follows: two asterisks—less than 1 chance in 100 that the observed value would occur if the true value were zero; one asterisk—between less than 1 chance in 20 and 1 in 100; no asterisk—more than one one chance in 20 that the true value would be zero.)

Group	Number	Log of area in 0.1 acres		Log of pounds per acre		Cross products	Regression *b*
		Sum	Sum of squares	Sum	Sum of squares		
A	13	68.571	367.903227	29.871	70.150311	157.666777	0.0171
B	21	28.997	43.277647	52.694	133.460644	73.001903	0.0746
C	27	28.114	43.496210	68.605	175.752785	72.676280	0.0872
D	18	26.511	42.284259	40.958	95.111962	58.812922	−0.4669**
E	10	12.458	15.646390	24.834	61.984514	30.978701	0.3209
F	5	7.958	15.352868	11.254	25.580738	17.480184	−0.1607
G	20	13.894	12.809294	41.117	85.965521	28.128203	−0.1380
H	3	11.708	48.176642	7.465	18.692913	29.673297	0.0563
B–C	48	57.111	86.773857	121.299	309.213429	145.678183	0.1536**

Group	References	Classification	Area in acres	Standing crop in pounds per acre			
				Range	Sum	Sum of squares	Mean
A	10, 13, 19, 24, 43, 68, 73	Rotenone of coves—south	470–260,000	28–623	3,330	1,230,106	256.2
B	4, 9, 31	Drain—midwest	0.75–12.5	71–778	7,829	3,709,447	372.8
C	3, 4, 5, 11, 30 33, 47, 54, 60	Poison—midwest	0.12–130.0	112–1,235	10,748	5,573,566	398.1
D	64	Drain—balanced ponds, Alabama	1.3–29.0	31–474	4,241	1,309,743	235.6
E	64	Drain—, unbalanced ponds, Alabama	1.2–2.6	134–492	3,281	1,210,685	328.1
F	7, 14, 42, 66, 69	Drain or poison ponds —south	1.8–72.0	98–432	815	237,681	203.8
G	20, 53	Mark and recovery—Iowa	0.1–4.88	28–370	2,733	514,447	136.7
H	69, 71, 78	Mark and recovery—California and Illinois	42.6–5,000	162–450	1,012	388,744	337.3

TABLE II. Standing crops of fish in natural lakes of the United States and Canada, in relation to area.

Group	Number	Log of area in 0.1 acres		Log of pounds per acre		Cross products	Regression b
		Sum	Sum of squares	Sum	Sum of squares		
A	10	13.517	21.398511	25.490	66.717684	34.278801	−0.0563
B	5	9.404	18.467538	8.706	15.536690	15.912925	−0.5911
C	12	24.284	50.783314	24.256	51.076186	48.525988	−0.3414
D	10	29.924	93.529402	19.649	39.980875	59.244502	0.1121
E	17	31.552	60.178050	27.407	45.820595	50.171936	−0.4299
F	6	15.909	42.759285	8.168	11.570418	21.191320	−0.8078
G	1	3.505	12.285025	1.243	1.545049	4.356715	...
BCD	27	63.613	162.780254	52.611	106.593751	123.683415	−0.0209
H	10	19.896	41.418944	−1.768	3.085998	−4.604834	−0.5929
I	5	17.586	62.815754	1.616	.666896	5.648127	−0.0371
J	2	5.728	17.226754	1.945	2.793337	4.709617	...

Group	References	Classification	Area in acres	Standing crop in pounds per acre			
				Range	Sum	Sum of squares	Mean
A	4, 27, 67, 74, 75, 76, 77	River backwaters and oxbows—Alabama to Wisconsin	0.1–11.9	40–1,145	4,984	3,605,886	498.4
B	37	Poison—Florida lakes	2.1–24.0	22.2–110	331	28,383	66.2
C	1, 23, 34, 35, 40	Poison—midwest lakes	0.8–27.1	19.4–370	1,816	422,974	151.3
D	15, 22, 26, 32, 46, 48, 51	Mark and recovery—midwest lakes	28.5–3060	31–342	1,288	266,988	128.8
E	1, 18	Poison—trout lakes, Michigan	1.6–21.9	10–137.3	889	69,488	52.3
F	56, 57, 58, 59	Poison—trout lakes, E. Canada	10.5–113	9.7–70.8	171	7,397	28.5
G	45	Mark and recovery—trout lakes, Alberta	320	...	17.5	306	17.5
BCD			0.8–3060	19.4–370	3.435	718,345	127.2
H	1, 36, 56	Poison—trout lakes, only trout considered	1.6–55.8	0.1–8.4	14.5	76.07	1.4
I	21, 28	Netting—trout lakes, only trout considered	100–1040	1.2–4.2	11.5	31.49	2.3
J	45, 50	Mark and recovery—trout lakes, only trout considered	16.7–320	2.0–44.0	46	1940	23.0

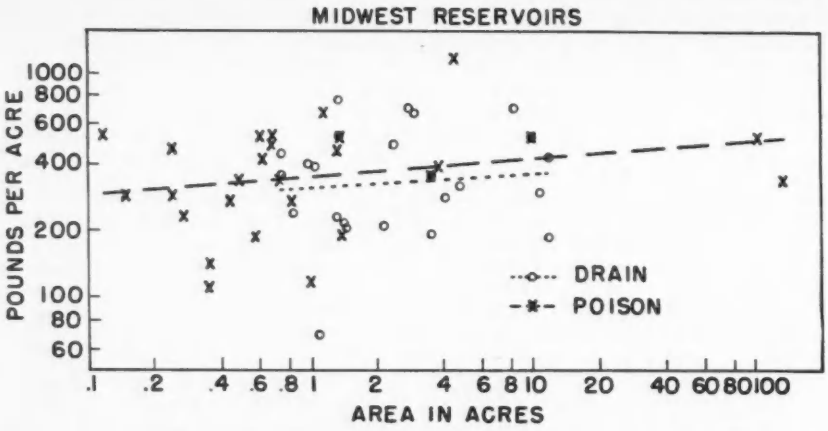

FIGURE 2. Relation of standing fish crop to area for midwestern reservoirs, showing separately results obtained by poisoning and by draining. (See also Table III.)

TABLE III. Analysis of variance for testing the difference between the standing crop of fishes in midwestern reservoirs as estimated by draining and by poisoning.

	Number	Logarithms of pounds per acre		
		Sum	Sum of squares	Sum of squared deviations
Drain	21	52.694	133.460644	1.238852
Poison	27	68.605	175.752785	1.432562
Combined	48	121.299	309.213429	2.683275

Source of variation	Degrees of freedom	Sum of squares	Mean square	
Total	47	2.683275		
Between	1	.011861	0.011861	
Within	46	2.671414	0.058074	F = 0.2

estimates for a series of Iowa ponds were strikingly different from the draining and poisoning estimates of midwestern reservoirs, however (Table I, groups B, C, G). Marking and recovery estimate usually refer only to fish over 5 or 6 inches in length whereas the draining and poisoning figures may also include smaller fishes. Population estimates made by rotenoning coves of larger reservoirs gave lower standing crops than poisoning or draining of smaller reservoirs, but the differences may have been due to factors other than the sampling techniques.

River backwaters and oxbows had average standing crops of almost 500 pounds per acre; midwestern reservoirs, almost 400 pounds per acre; other reservoirs and ponds, 200 to 300 pounds per acre; warm-water lakes, 125 to 150 pounds per acre; and trout lakes, up to about 50 pounds per acre.

TABLE IV. Standing crops of fish in relation to maximum depth of body of water.

References	Classification	Logs of depth in feet			Logs of pounds per acre		Cross products	Regression *b*	Depth in feet	Standing crop in pounds per acre
		Number	Sum	Sum of squares	Sum	Sum of squares				
1, 18, 45, 56, 58, 59	Trout lakes	21	31.599	48.552117	32.224	51.486356	47.919001	−0.5662	9.8–90	9.7–137.3
1, 15, 22, 26, 32, 35, 37, 40, 46, 48	Warmwater lakes	24	31.101	42.939625	44.953	87.081937	57.110823	−0.4333*	3–60	22.2–279.0
3, 4, 5, 11, 31, 33,	Reservoirs	20	21.321	27.233831	50.315	127.829179	54.005877	+0.0816	3.5–30	112–1,235
54, 60	Reservoirs[a]	19	19.020	21.939230	47.224	118.274898	46.893486	−0.1311	3.5–30	112–657

[a]Leaving out one gravel pit with a high population of buffalo fish [11].

TABLE V. Standing crops of fish in relation to methyl orange alkalinity.

References	Classification	Number	Logs of methyl orange alkalinity in p.p.m.		Log of pounds per acre		Cross products	Regression *b*	Methyl orange alkalinity p.p.m.	Standing crop in pounds per acre
			Sum	Sum of squares	Sum	Sum of squares				
1, 50, 56	Trout lakes	16	27.247	52.487475	25.539	42.173361	45.023331	0.2517*	5–208	10.0–111.5
1, 23,26, 32	Warmwater lakes	9	14.562	26.530020	15.445	27.694977	26.186643	0.4031	3–165	19.4–194.5
4, 31, 42, 47, 53	Reservoirs	7	13.713	27.398691	15.811	35.947857	31.269192	0.5523*	30–178	113.0–341.0

The regressions of standing crop per acre on the area of the lakes and reservoirs were negative in 11 out of 17 cases and positive in 6, but in only 2 cases was the regression coefficient, *b*, significantly different from zero at the 95 per cent confidence level (Fig. 3). In the combined drained and poisoned midwest reservoir estimates there was a significant *positive* regression with the standing crop per acre, increasing with increased area of the reservoir. A significant *negative* regression was found in a series of Alabama ponds, varying in area only from 1.3 to 29.0 acres. The conclusion must, therefore, be made that the available data show no significant correlation between standing crop and area of the body of water.

RELATION OF STANDING CROP TO DEPTH OF BODY OF WATER

In general the productivity of a lake increases as the mean depth of the lake decreases (see Rawson [44]). Mean depth records are available for only a few of the lakes from which standing crop estimates have been reported, but maximum depths are recorded for a fair number (Table IV). The trout lakes show a negative regression of standing crop on the maximum depths of the lakes, but the regression value *b* is not quite large enough to be significant at the 95 per cent level of significance (the computed *t* value is 1.89 when 2.09 would be significant at the 95 per cent level). The regression in the warm-water lakes is significant at the 95 per cent level. The regression value *b* is positive in the series of reservoirs, but this situation seems to be due to a 20-foot gravel pit with a high population of buffalo fish [11]. If this one pond is eliminated as not

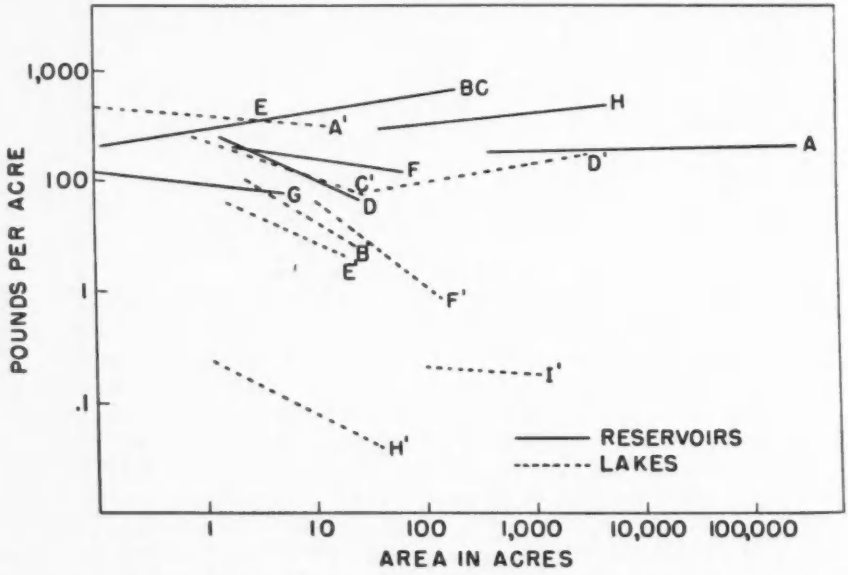

FIGURE 3. Regressions of logarithm of standing fish crop on logarithm of area of body of water. (See also Tables I and II.)

typical, the regression is negative, but not significant at the 95 per cent level of significance. Differences in depth explain about 16 per cent of the variation of standing crops in the trout lakes and in the warm-water lakes, but only about 5 per cent of the variation in the reservoirs, even excluding the gravel pit.

RELATION OF STANDING CROP OF FISH TO CARBONATE CONTENT OF THE WATER

The only other quantitative data that were recorded from enough lakes or reservoirs to permit a test of the correlation with standing crop was the methyl

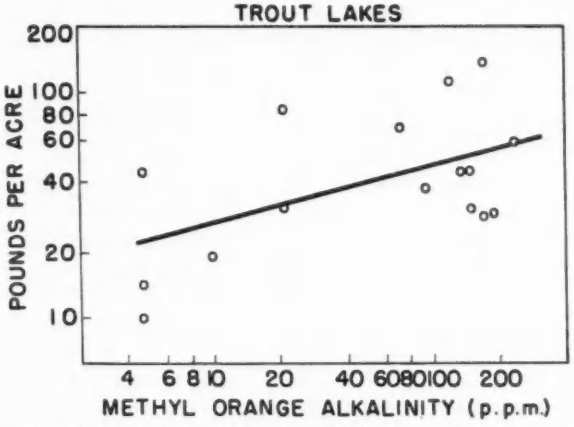

FIGURE 4. Relation of fish crop in trout lakes to methyl orange alkalinity. (See also Table V.)

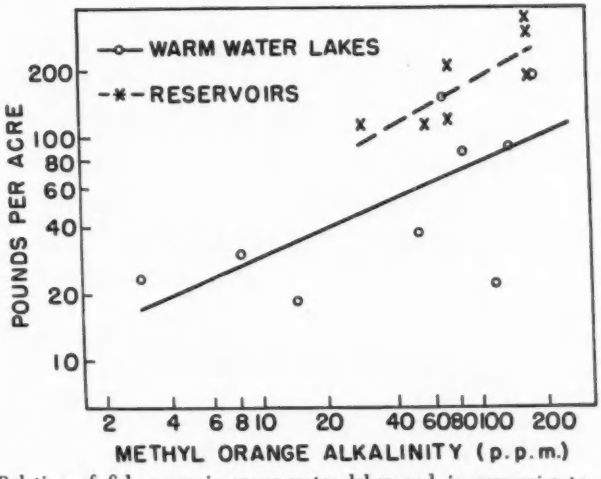

FIGURE 5. Relation of fish crops in warm-water lakes and in reservoirs to methyl orange alkalinity. (See also Table V.)

orange alkalinity or carbonate content of the water (Table V, Fig. 4, 5). The standing crop per acre showed a significant increase with increased alkalinity in trout lakes, in warm-water lakes, and in reservoirs. About 28, 41 and 69 per cent of the variation in standing crop of the three groups of lakes, respectively, could be explained by the differences in methyl orange alkalinity or associated factors (coefficients of correlation r of 0.52, 0.64 and 0.83, respectively).

PYRAMID OF NUMBERS AND HABITAT SEGREGATION

An analysis of the standing crop per acre by species (Fig. 6, Tables VI, VII, VIII) gives further evidence of the well-known phenomenon often referred to as the Eltonian pyramid of numbers. The species with relatively short food chains, such as the gizzard shad, buffalo, carp, and suckers, have rather high standing crops; small insectivorous fishes, such as bluegills, other sunfishes and crappies, have intermediate standing crops; and the secondary predators, such as the largemouth bass, walleyes, and pike, have relatively low standing crops. Trout may belong in the insectivorous or predator group in various lakes.

At each level in the pyramid there are species which have much lower average standing crops and never seem to attain the predominance that is characteristic of other species in the same level of the food chain. For example, the carp suckers, the warmouth, and the rockbass are usually secondary species, found in lakes with other more abundant species at their same food level.

The fact that these species are at the same food level does not necessarily mean that they are in competition. The presence of the two or more species in the lake for many years is evidence that the competition between the species is not complete. According to Gause's principle (see [41], p. 171) there cannot be more than one species per ecological niche.

The degree of competition may vary from almost complete to negligible, even for species that appear to be much the same in their general requirements. Competition may be mitigated by slight differences in the niches or by habitat segregation. One example of habitat segregation in fishes has been reported by Dendy [16, 17] in Norris Reservoir, Tennessee, where several species were in different strata of the water presumably because of temperature selection. The largemouth bass was largely in water over 80°F. and the spotted bass in water of 70 to 78°F. The walleye was usually in water 70 to 76°F., while the sauger was in water of 60 to 70°F.

Competition may also be decreased through differences in diurnal cycles of fish. For example, in Lake of the Woods, Minnesota, and in Clear Lake, Iowa, the walleye was found to forage largely at night and the northern pike in the daytime [12].

Svärdson [63] has reported that very similar species of whitefishes (*Coregonus* spp.) maintain themselves in the same lakes through differences in spawning seasons or spawning sites.

Other examples of habitat segregation could be mentioned, but I think that it must be admitted that our knowledge of the effect of this phenomenon upon fish production is extremely limited.

Presumably fish production will increase as the number of niches increases, unless the production of all the species is limited by a single factor. We generally cannot determine the number of available niches in a habitat, but probably the proportion of occupied niches increases as the number of species of fishes increases. A plotting of the standing crop per acre in the midwestern reservoirs reveals that there is the expected increase in standing crop with increase in the

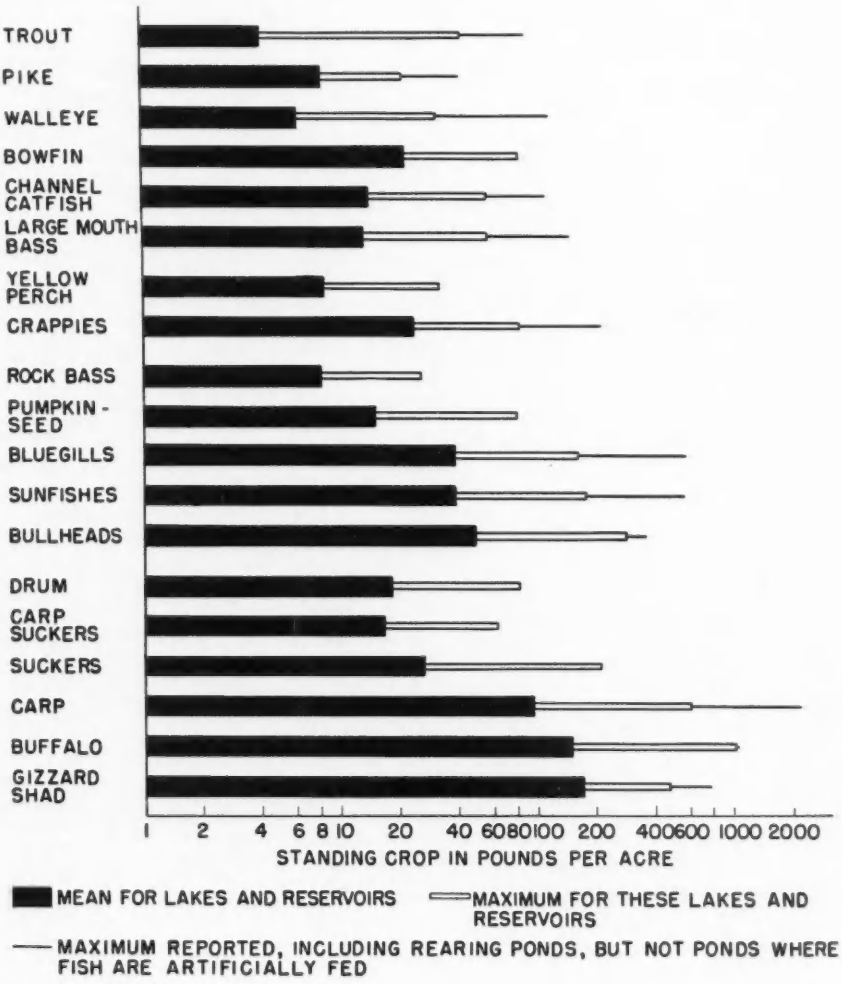

FIGURE 6. Standing crops of fish per acre, by species. (See also Tables VI–VIII.)

TABLE VI. Standing crop, in pounds per acre, of fish with short food chains.

Species and habitat	Number	Mean	Range	References
GIZZARD SHAD				
Lakes, Indiana to Wisconsin	7	100.1	0.9–408.0	27, 32, 74, 75, 76
Reservoirs, Oklahoma to Illinois	15	204.4	25.9–468.1	4, 13, 19, 24, 33, 43, 68, 73
Ponds, Alabama	6	346.3	47.7–758.4	64
BUFFALO FISH				
Lakes, Indiana to Wisconsin	8	134.2	0.1–884.0	4, 27, 32, 74, 75, 76
Minnesota rough fish lakes	20	166.6	–1,144.0	39
Minnesota game fish lakes	4	4.3	–11.9	39
Reservoirs, Texas to Illinois	17	161.0	0.5–1,016.3	4, 5, 7, 11, 13, 33, 43, 68, 73
SMALLMOUTH BUFFALO				
Texas to Illinois	11	51.4	1.0–290.2	4, 7, 13, 32, 43, 68, 73, 74
BIGMOUTH BUFFALO				
Oklahoma to Wisconsin	17	173.7	0.5–1,016.3	4, 11, 32, 33, 43, 68, 74, 75, 76
BLACK BUFFALO				
Oklahoma to Illinois	13	22.0	2.2–88.7	4, 43, 68, 74
CARP				
Lakes, Illinois and Wisconsin	11	142.9	0.1–609.3	4, 27, 40, 74, 75, 76
Minnesota rough fish lakes	43	202.6	–2,222.0	39
Minnesota game fish lakes	36	11.0	–35.2	39
Reservoirs, Oklahoma to Illinois	24	73.3	4.6–232.6	4, 5, 11, 13, 24, 33, 42, 43, 60, 68, 73
CHUB SUCKER				
Lakes and reservoirs, Florida to Wisconsin	7	21.7	0.6–72.0	37, 40, 61
Ponds, Alabama	10	14.0	0.1–43.3	64, 66
SPOTTED SUCKER				
Alabama to Wisconsin	8	7.8	2.6–17.8	5, 13, 27, 43, 64, 75
REDHORSE				
Lakes and reservoirs, Tennessee to Wisconsin	5	7.5	0.5–22.0	19, 42, 43, 75
COMMON SUCKER				
Lakes and reservoirs, Oklahoma to Michigan	10	10.9	0.1–31.5	1, 4, 40, 42, 60, 64, 73, 76
SUCKERS AND REDHORSE				
Lakes, Florida to Alberta	18	16.7	0.1–72.0	1, 27, 32, 37, 40, 45, 56, 74, 75, 76
Reservoirs, Texas to Massachusetts	17	37.6	0.6–212.5	4, 7, 11, 13, 19, 31, 42, 43, 60, 61, 66, 68, 69, 73
Alabama ponds	12	7.6	0.1–34.7	64
Minnesota rough fish lakes	23	7.9	–91.0	39
Minnesota game fish lakes	34	9.8	–102.3	39
GOLDEN SHINER				
Lakes, Alabama to Nova Scotia	9	4.5	0.1–33.0	1, 27, 56, 57, 67, 74, 75
Reservoirs, Texas to Massachusetts	16	42.9	0.3–327.0	33, 42, 60, 61, 69, 4, 5, 14
Ponds, Iowa and Alabama	14	14.9	0.2–100.0	20, 64

TABLE VI. (*Continued*)

Species and habitat	Number	Mean	Range	References
MINNOWS, INCLUDING TOP-MINNOWS				
Lakes, Florida to Nova Scotia	34	4.7	0.1–33.0	1, 27, 37, 56, 57, 59, 67, 74, 75, 76
Reservoirs, Texas to Massachusetts	18	39.4	0.3–327.0	4, 5, 13, 14, 19, 33, 42, 60, 61, 69
Ponds, Iowa and Alabama	22	21.6	0.2–100.0	20, 64
DRUM				
Lakes, Illinois and Wisconsin	5	6.9	3.0–14.2	74, 75, 76
Reservoirs, Oklahoma to Illinois	6	27.8	1.2–81.8	4, 13, 24, 43, 68, 73

TABLE VII. Standing crop, in pounds per acre, of fish with intermediate food chains.

Species and habitat	Number	Mean	Range	References
BLUEGILL				
Lakes, Indiana to Wisconsin	20	30.2	0.2–113.1	1, 22, 27, 40, 46, 51, 74, 75, 76
Reservoirs, mostly midwestern	35	42.3	3.3–180.4	4, 7, 11, 13, 19, 33, 42, 47, 53, 60, 61, 66, 68, 73, 78
Ponds, Iowa	16	66.7	13.0–182.2	20
Managed ponds, Texas to Michigan	38	197.2	7.0–584.0	2, 6, 8, 61
Ponds, Alabama	110	246.6	5.6–465.0	64, 65
GREEN SUNFISH				
Lakes, Michigan and Indiana	3	2.9	0.5–7.4	1, 22
Reservoirs, Texas to Indiana	21	10.4	0.1–44.9	4, 5, 7, 13, 33, 42, 43, 47, 53, 68, 73
Ponds, Alabama to Iowa	20	72.6	0.3–343.6	3, 20, 64
PUMPKINSEED				
Lakes, Indiana to Minnesota	15	11.3	0.1–81.2	1, 22, 23, 76
Reservoirs, Massachusetts and Michigan	4	27.2	0.1–52.5	31, 62
REDEAR SUNFISH				
Lakes and reservoirs, Tennessee and Indiana	3	4.0	0.1–8.3	22, 42, 47
Ponds, Alabama	17	57.2	0.4–186.5	64
ORANGESPOT SUNFISH				
Oklahoma to Wisconsin	10	0.8	0.1–3.9	4, 13, 68, 73, 74, 75
ROCK BASS				
Tennessee to Michigan	10	8.2	0.3–26.3	1, 31, 42
WARMOUTH				
Lakes and reservoirs, Florida to Iowa	23	4.4	0.1–25.0	4, 7, 13, 22, 37, 43, 46, 60, 68, 73, 74
Ponds, Alabama	5	16.1	0.1–55.7	64
LONGEAR SUNFISH				
Oklahoma to Kentucky	4	3.1	1.7–7.0	13, 42, 43, 73

TALLE VII. (*Continued*)

Species and habitat	Number	Mean	Range	References
ALL THE ABOVE SPECIES				
Lakes	35	28.1	7.8–113.1	
Reservoirs	45	46.2	0.2–180.9	
Ponds	65	153.4	7.5–584.0	
Ponds, Alabama	111	254.8	5.6–465.0	
WHITE CRAPPIE				
Lakes, Indiana to Wisconsin	6	8.9	0.8–35.2	27, 32, 74, 75
Reservoirs, Texas to Illinois	25	26.2	0.9–85.0	4, 5, 7, 13, 24, 33, 42, 43, 66, 68, 73
Ponds, Alabama	16	29.3	0.9–130.2	64
BLACK CRAPPIE				
Lakes, Indiana to Wisconsin	10	10.1	2.0–34.3	4, 27, 32, 40, 74, 75
Minnesota rough fish lakes	34	45.0	–643.0	37
Minnesota game fish lakes	60	28.3	–273.3	37
Reservoirs, California to Tennessee	15	13.8	0.1–53.5	4, 13, 19, 33, 42, 68, 78
Ponds, Alabama and Missouri	7	104.8	53.9–219.2	3, 64
CRAPPIES COMBINED				
Lakes	13	17.5	3.0–39.0	
Reservoirs	30	30.9	1.0–85.0	
Ponds	33	44.0	0.9–219.2	
YELLOW PERCH				
Lakes, Iowa to Nova Scotia	27	9.1	0.1–34.6	1, 18, 23, 26, 40, 46, 51, 56, 57, 75, 76
Minnesota rough fish lakes	21	8.1	–111.6	39
Minnesota game fish lakes	41	32.1	–184.0	39
Reservoirs, Illinois and Massachusetts	4	5.0	0.1–15.6	4, 60, 61
WHITE PERCH				
Massachusetts and Nova Scotia	4	11.8	5.5–17.7	56, 57, 61
BULLHEADS				
Lakes, Alabama to Nova Scotia	18	30.2	0.1–188.2	1, 4, 23, 27, 46, 51, 57, 58, 67, 74, 75, 76
Minnesota rough fish lakes	34	17.7	–133.6	39
Minnesota game fish lakes	41	14.7	–144.2	39
Reservoirs, mostly midwestern	30	60.3	0.1–292.1	4, 5, 11, 13, 24, 33, 42, 46, 53, 60, 61, 66, 68, 72, 78
Ponds, Alabama to Iowa	39		0.2–358.0	3, 20, 30, 64

TABLE VIII. Standing crop, in pounds per acre, of fish with long food chains.

Species and habitat	Number	Mean	Range	References
LARGEMOUTH BASS				
Lakes, Florida to Wisconsin	30	7.1	0.2–20.7	1, 4, 22, 27, 32, 37, 40, 46, 74, 75, 76
Minnesota game fish lakes	55	8.5	–30.5	39
Minnesota rough fish lakes	29	9.6	–66.5	39
Reservoirs, Texas to Massachusetts	34	19.2	0.1–59.0	4, 7, 9, 11, 13, 19, 24, 29, 31, 33, 42, 43, 46, 60, 61, 66, 68, 69, 73

TABLE VIII. (*Continued*)

Species and habit	Number	Mean	Range	References
Ponds, Texas to Michigan	166	56.1	0.3–155.0	2, 6, 8, 20, 53, 62, 64, 65, 72
SAMLLMOUTH BASS				
Tennessee to Wisconsin	6	4.2	0.04–11.8	4, 19, 40, 42, 46, 60
SPOTTED BASS				
Tennessee to Missouri	4	0.9	0.2–1.6	13, 19, 42, 43
REDEYE BASS				
Alabama	1	8.5		66
WHITE BASS				
Oklahoma to Wisconsin	11	3.2	0.1–23.1	13, 27, 43, 51, 68, 73, 74, 75, 76
YELLOW BASS				
Tennessee to Iowa	7	5.3	0.3–20.1	4, 11, 13, 33, 68, 74
BOWFIN				
Tennessee to Wisconsin	7	21.6	3.4–84.3	27, 68, 74, 75, 76
GAR				
Florida to Wisconsin	11	9.2	0.01–49.0	4, 13, 24, 37, 68, 73, 74, 75, 76
EEL				
New Brunswick and Nova Scotia	5	15.4	0.2–70.8	55, 57, 59
CHANNEL CATFISH				
Lakes, Illinois to Wisconsin	7	18.8	1.1–53.1	27, 51, 74, 75, 76
Reservoirs, Alabama to Iowa	10	13.9	4.0–57.0	4, 11, 13, 19, 24, 33, 43, 66, 68, 73
Ponds, Alabama and Texas	4	82.6	7.3–116.2	8, 64
FLATHEAD CATFISH				
Oklahoma to Wisconsin	5	22.2	1.4–92.4	13, 24, 64, 73, 75
NORTHERN PIKE				
Lakes, Illinois to Minnesota	7	8.2	0.01–21.8	23, 27, 51, 74, 75, 76
Minnesota game fish lakes	59	8.0	–42.5	39
Minnesota rough fish lakes	30	5.4	–29.2	39
MUD PICKEREL				
Indiana and Michigan	3	1.0	0.8–1.2	1, 47
CHAIN PICKEREL				
Massachusetts	2	4.3	2.0–6.5	61
WALLEYE				
Lakes, Iowa to Michigan	7	6.2	0.4–33.0	1, 27, 51, 74, 75
Minnesota game fish lakes	25	8.1	–54.5	39
Minnesota rough fish lakes	14	7.0	–21.1	39
Reservoirs, Iowa	1	0.2		60
Rearing ponds, Minnesota	44	38.7	–121.0	38
SAUGER				
Tennessee to Wisconsin	5	1.8	0.4–5.6	13, 19, 27, 75
TROUT				
Lakes, Wyoming to Nova Scotia	18	4.1	0.1–44.0	1, 28, 36, 45, 50, 56, 57
Managed lakes, Wisconisn	8	43.5	9.0–92.0	25
MOUNTAIN WHITEFISH				
Alberta	1	6.9		45
ALL COMBINED				
(except rearing ponds)	187	44.3	0.1–187.3	

number of species present (Fig. 7, Table IX). The regression may be described as:

$$P = 2.302 + 0.3243\,N$$

where P is the logarithm of the standing crop in pounds per acre
and N is the logarithm of the number of species in the population.

The relationship between standing crop and number of species is not so clearly demonstrated in several pond studies (Tables X) but the trends are

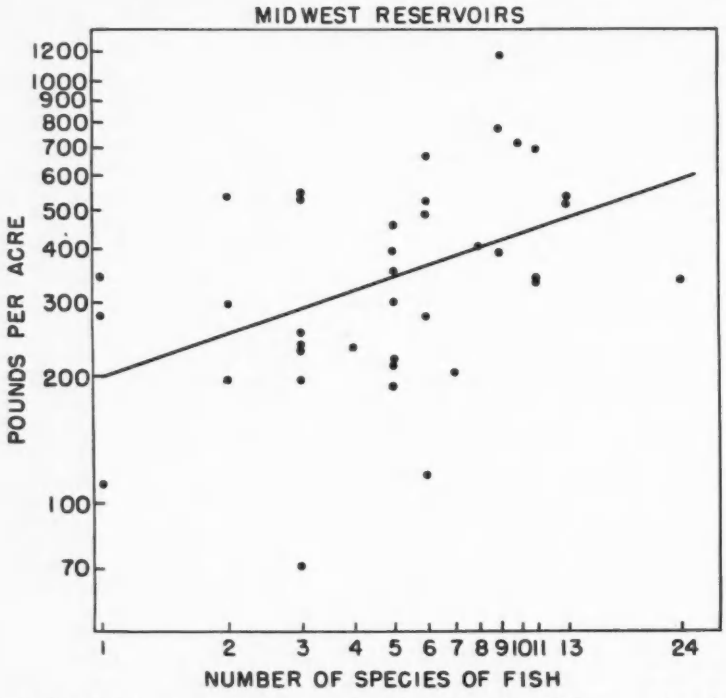

FIGURE 7. Relation between standing crops and numbers of species of fish present in midwestern reservoirs. (See also Table IX.)

TABLE IX. Standing crop of fish per acre in midwestern reservoirs in relation to number of species present.

References	Number	Log of number of species		Log of pounds per acre		Cross products	Regression b	Standard error s_b
		Sum	Sum of squares	Sum	Sum of squares			
3, 4, 5, 9, 11 30, 32, 44, 51, 57	38	25.968	21.570754	95.859	244.157633	66.747548	0.3243**	0.1187

similar. In these studies, however, ponds with two species frequently had higher standing crops than ponds with several species.

Although production probably increases as the number of filled niches increases, the maximum production of a particular species may be reached in a habitat with no other species, at least at the same food level, even though some of the niches may thereby be left vacant. In the pond studies (Table X) the average standing crop of the selected species was in every case lower in ponds with more than two species than in those with only two and in most cases was lower in ponds with two species than in those with one. The second species was at a different food level from the selected species in all except the bullhead ponds. The additional species were sometimes at the same food level.

TABLE X. Standing crop, in pounds per acre, as the number of species is increased in ponds.

References	Pond type and species A		Species A alone	Species A plus one other[a]	Species A plus others[a]
8	Texas ponds,	Number	3	10	1
	largemouth bass	Mean	70.5	146.7 (54.7)	156.8 (50.2)
		Range	50–94	59–249 (25–131)	
6	Ridge Lake, Ill.,	Number	1		3
	largemouth bass	Mean	48.7		159.6 (40.5)
		Range			72–256 (31–50)
61, 62	Alabama balanced	Number	1	35	34
	ponds,	Mean	81.0	342.8 (80.1)	297.8 (49.2)
	largemouth bass	Range		137–464 (29–155)	32–611 (1–134)
61, 62	Alabama unbalanced	Number		20	17
	ponds,	Mean		395.8 (58.1)	417.5 (43)
	largemouth bass	Range		18–514 (17–95)	91–1080 (6–95)
61, 62,	Alabama ponds,	Number	15	54	56
63	bluegill	Mean	305.6	370.4 (331.7)	335.3 (196.8)
		Range	47–588	137–514 (80–465)	91–100.0 (6–388)
20	Iowa ponds, bullheads	Number	1	2	7
		Mean	134.0	287.5 (92.5)	128.8 (64.4)
		Range		205–370 (59–126)	54–288 (11–236)

[a]Numbers in parentheses refer to species A in these same lakes.

INTERSPECIFIC COMPETITION

Interspecific competition is defined by Odum ([41], p. 165) as those interactions "in which each population adversely affects the other in the struggle for food, nutrients, living space or other common need". The principal criterion which Odum (p. 170) uses in recognizing competition is a difference in the growth curves of the populations. If the observed growth curves "of the two populations are steeper when they are separate than when they are interacting, competition of some sort is operating". Comparison of population growth curves may be possible with experimental populations such as Protozoa or meal worms, but such comparisons for fish populations will have to await the development of much more exact techniques of sampling and of interpretation.

TABLE XI. Standing crop of largemouth bass, in pounds per acre.

Group	References		Number	Sum	Sum of squares	Mean	Range
		RESERVOIRS					
A	4, 11, 28, 45, 57	Midwest, poisoned, Indiana to Iowa	7	182.8	8,411.56	26.1	2.5– 59.0
B	4, 9, 30, 32	Midwest, drained, Missouri to Michigan	15	359.4	11,763.06	24.0	9.8– 44.3
C	7, 40, 63, 66	South, drained and poisoned	4	30.4	289.66	7.6	3.5– 13.1
D	13, 19, 24, 41, 58, 65, 70	Rotenone of coves, Oklahoma to Massachusetts	8	79.2	1,148.70	9.9	0.1– 19.3
E	20, 50, 69	Ponds, mark and recovery, Illinois and Iowa	15	242.5	6,449.81	16.2	0.3– 37.8
		MANAGED PONDS: BASS, BLUEGILL					
F	2	Michigan	12	992.0	97.822.00	82.7	36.0–151.0
G	61, 62	Alabama, balanced	36	2,882.3	271,963.91	80.1	29.5–155.0
H	61, 62	Alabama, unbalanced	19	1,145.3	76,350.35	60.3	23.5– 95.0
I	8, 59	Texas and West Virginia	17	810.3	49,803.87	47.7	25.0–130.5
		MANAGED PONDS: BASS ONLY					
J	8	Texas	3	211.6	15,900.74	70.5	50.3– 94.1
		MANAGED PONDS: MIXED POPULATION					
K	6	Illinois	4	169.7	7,423.81	42.4	31.5– 50.4
L	61, 62	Alabama, balanced	34	1,672.7	108,693.99	49.2	1.4–133.9
M	61	Alabama, unbalanced	18	747.3	46,744.65	41.5	5.9–101.0
N	8, 59	Texas and West Virginia	8	426.2	24,825.72	53.3	28.9– 74.5
		WARM-WATER LAKES					
O	4, 26, 71, 72, 73	Oxbows, Illinois and Wisconsin	7	36.7	311.11	5.2	0.4– 10.5
P	36	Florida	5	46.2	535.32	9.2	3.0– 16.0
Q	1, 38	Poisoned, Michigan and Wisconsin	4	42.2	531.70	10.6	2.8– 15.1
R	22, 31, 38	Mark and recovery, Indiana	3	28.4	469.18	9.5	1.5– 20.7
		TROUT LAKES					
S	1	Poisoned, Michigan	11	58.6	607.60	5.3	0.2– 19.0
		COMBINED	230	10,174.2	730,046.74	44.2	0.1–155.0

TABLE XII. Analysis of variance of the standing crop of largemouth bass from various types of lakes and ponds, as classified in Table XI.

Source of variation	Degree of freedom	Sum of squares squares	Mean square	F
Total	229	279,984.37		
Between types	18	148,503.94	8,250.22	
Within	211	131,480.43	623.13	13.2**
Managed bass-bluegill ponds only (groups F, G, H, I of Table XI). Between types	3	15,817.79	5,272.60	8.4**
Midwest reservoirs (groups A and B of Table XI). Between poisoned and drained	1	22.14	22.14	0.03
Reservoirs (groups A, B, C, D, E of Table XI). Between types	4	2,008.56	502.14	0.8

TABLE XIII. Standing crops, in pounds per acre, of largemouth bass in midwest reservoirs with and without certain other species.

	Number	Sum	Sum of squares	Mean	F
Without	19	491.9	18,143.95	25.9	
With small mouth bass, pike, gar and walleye	3	50.3	2,030.67	16.8	0.65
Without	16	450.7	17,482.45	28.2	
With above predators+channel catfish	6	91.5	2,692.17	15.3	2.39
Without	18	456.1	17,503.11	25.3	
With channel catfish	4	81.1	2,677.51	21.5	0.14
Without	7	167.1	5,977.51	23.9	
With crappies	15	375.1	14,197.11	25.0	0.02
Without	11	306.5	11,112.47	27.9	
With bullheads	11	235.7	9,062.15	21.4	0.69
Without	9	295.9	13,204.83	32.9	
With carp	13	246.3	6,969.79	18.9	3.57
Without	12	318.3	12,646.77	26.5	
With buffalo	10	224.9	7,527.85	22.5	0.41
Without	13	372.3	16,113.13	28.6	
With gizzard shad	9	169.9	4,061.49	18.9	1.61
Without	5	168.3	8,040.11	33.7	
With rough fish	17	373.9	12,134.51	22.0	1.67

TABLE XIV. Regressions of standing crops of largemouth bass on standing crops of other species in midwest reservoirs.

Other species	Logarithms of standing crops in 0.1 pounds per acre						Regression b	s_b	Intercept a	Corresponding pounds per acre, 95% confidence interval[a]
	Largemouth bass			Cross products	Other					
	Number	Sum	Sum of squares		Sum	Sum of squares				
Predators, including channel catfish	6	11.770	24.336394	19.843092	9.806	19.341736	0.1831	0.2927	1.669	...
Crappies	15	34.089	79.352479	85.403039	37.308	94.471118	0.3675	0.2754	1.359	...
Bullheads	11	23.443	52.133625	47.756951	22.513	52.505429	−0.0356	0.1934	2.204	...
Sunfishes	22	49.659	115.223329	136.750377	59.492	165.821592	0.4928**	0.1381	1.885	0.7–79.5
Sunfishes, crappies, yellow bass, minnows	22	49.659	115.223329	148.805056	65.103	195.260817	0.6995**	0.1864	0.188	0.08–3.2
Carp	13	28.272	62.758368	75.368159	35.303	98.950581	−0.4569**	0.1363	3.416	27.1–250.7
Buffalo	10	22.581	51.788247	64.368229	28.485	89.099689	0.0030	0.1118	2.258	...
Gizzard shad	9	20.113	45.226335	65.181520	29.178	95.945550	−0.0184	0.1714	2.269	...
Rough fish	17	38.036	86.823558	127.160075	57.356	197.552982	−0.2893	0.1511	3.2131	...

[a]Only given where the regression value differs from zero at the 95 per cent confidence level or better.

TABLE XV. Standing crops, in pounds per acre, of bluegills in midwest reservoirs, with and without certain other species.

	Number	Sum	Sum of squares	Mean	F
Without	12	758.3	82,524.79	63.2	
With green sunfish	9	447.1	52,946.77	49.7	0.27
Without	7	339.5	35,794.15	48.5	
With sunfishes and perch	14	866.3	99,684.85	61.9	0.24
Without	5	308.6	36,200.06	61.7	
With crappies	16	897.2	99,278.94	56.1	0.03
Without	8	690.5	78,706.67	86.3	
With bullhead	13	515.3	56,772.33	39.6	4.99*
Without	12	689.1	80,523.83	57.4	
With gizzard shad	9	516.7	54,868.47	57.4	0.0
Without	6	536.6	68,266.04	89.4	
With carp	15	669.2	67,212.96	44.6	2.84
Without	4	276.4	32,868.34	69.1	
With rough fish	17	929.4	102,523.96	54.7	0.20

(See p. 564 for Table XVI.)

TABLE XVII. Standing crops, in pounds per acre, of certain species of fishes in midwest reservoirs, and the significance of mean differences between crops when another species is, or is not, present.

	Number	Sum	Sum of squares	Mean	F
White crappie	9	317.7	20,008.37	35.3	
White crappie with black crappie present	9	242.0	8,668.98	26.9	0.46
Black crappie with white crappie present	9	154.1	5,029.87	17.1	
Black crappie	5	460.6	47,451.56	92.1	39.7**
Carp	8	721.8	108,125.98	90.2	
Carp with buffalo present	10	782.0	95,142.70	78.2	0.12
Buffalo with carp present	10	1845.8	1,154,863.42	184.6	
Buffalo	2	542.9	237,046.33	271.5	0.13

TABLE XVI. Regressions of standing crops of bluegill on standing crops of other species in midwest reservoirs.

Other species	Logarithms of standing crops in 0.1 pounds per acre						Regression b	s_b	Intercept a
	Bluegill			Cross-products	Other				
	Number	Sum	Sum of squares		Sum	Sum of squares			
Green sunfish	9	21.893	57.587421	31.972241	13.637	25.407961	−0.2530	0.3482	2.816
Sunfishes and perch	14	35.273	92.989923	60.866339	23.968	46.123262	0.0941	0.2583	2.358
Crappies	16	39.612	102.518658	97.648454	39.290	98.112826	0.2306	0.4371	1.910
Bullheads	13	29.583	70.620941	67.060843	29.970	77.056462	−0.1431	0.1893	2.606
Gizzard shad	9	23.091	60.871807	75.503576	29.160	95.823276	0.5121	0.3681	0.907
Carp	15	35.581	88.218167	97.652673	41.420	117.664738	−0.1818	0.2945	2.874
Rough fish	17	41.784	107.475540	138.756799	57.103	195.778845	−0.4019	0.2635	3.343

TABLE XVIII. Regressions of standing crops of one species on standing crops of another species in midwest reservoirs.

Species	Logarithms of standing crops in 0.1 pounds per acre						Regression b	s_b
	First species			Cross products	Second species			
	No.	Sum	Sum of squares		Sum	Sum of squares		
White crappie on black crappie	9	20.671	48.916257	35.732414	15.969	35.810783	−0.1264	0.1588
Carp on buffalo	10	27.403	76.949293	75.457060	27.578	83.395000	−0.0157	0.1778

Differences in the standing crops of one species in the absence and in the presence of another species may give some clues as to the amount of competition between the two species. The regression of the standing crop of one species upon the standing crop of another may provide further evidence.

Before we look at some of the available data, however, there are certain precautions that should be stated. The fact that there is a significant decrease in standing crop of one species when another species is present—and that the standing crop further decreases as the other species becomes more abundant—does not indicate that competition is taking place. The species may simply have different optimum conditions, with one species abundant when the environmental conditions favor it and the other species increasing as the environment becomes more favorable to it, but with neither species competing with the other. Thus, analysis of the standing crops may not give proof of competition, but may aid in determining where competition may be suspected.

Among the secondary predators the largemouth bass (Table XI) was the only species taken from enough waters to permit analysis for evidence of competition. It is obvious that the largemouth bass populations in the various types of lakes and reservoirs were different (Table XII) and that the analyses must therefore be made within a given type.[4] The midwest reservoirs, drained and poisoned, were selected for analysis. Populations with smallmouth bass, pike, gar, walleyes or channel catfish had smaller standing crops of largemouth bass than populations with no other large predator, but the difference was not quite significant at the 95 per cent confidence level (Table XIII). There was a positive regression of largemouth bass standing crops on standing crops of the other predators, rather than the negative regression which might have been expected if competition were the significant controlling factor, but the regression coefficient b was near zero and shows no significant correlation (Table XIV). Largemouth bass standing crops appear to be improved where crappies, sunfishes and other forage fishes are present. Carp, gizzard shad, and other rough fishes, on the other hand, seem to be associated with decreased bass crops. The buffalo seemed to have less effect on bass crops than the other rough fishes.

[4]To test whether the standing crops of bass per acre or the percentages which bass composed of the standing crops might be most representative of conditions in the various lakes the following data were computed:

	Number of lakes	*Mean*	*Standard variation*	*Coefficient of variation*
Reservoirs—Percentage	29	7.27%	7.48	104
—Standing crop	29	19.44 lb.	15.87	82
Oxbows—Percentage	7	1.71%	2.16	127
—Standing crop	7	5.26 lb.	4.51	86
Warm lakes—Percentage	12	17.51%	8.05	61
—Standing crop	12	0.77 lb.	5.94	61
Trout lakes—Percentage	11	10.89%	10.26	94
—Standing crop	11	4.48 lb.	5.34	119

These data indicate no particular superiority for either analysis. For the study of competition, the standing crop is the more logical measure.

Bluegill standing crops appeared to decrease with increase in green sunfish crops (Tables XV, XVI) but not with crops of all sunfishes and perch combined. Bullheads, carp and other rough fish appeared to be associated with decreased bluegill crops.

White and black crappies did better separately than in combination (Tables XVII, XVIII). Carp and buffalo also show possible competition.

Again, the precaution should be stated that these regressions give no proof of competition or protocooperation, but they may give clues as to where such phenomena may be found (Table XIX).

TABLE XIX. Species where the standing crops of one show indications of being affected by the presence of the other, midwest reservoirs.

Standing crops less	No evident difference	Standing crops more
Largemouth bass and bullheads	Largemouth bass and other predators	Largemouth bass and crappies
Largemouth bass and carp**	Largemouth bass and buffalo	Largemouth bass and sunfishes**
Largemouth bass and gizzard shad	Bluegills and crappies	Largemouth bass and forage fishes**
Largemouth bass and rough fish	Bluegills and gizzard shad	Bluegill and sunfishes and perch
Bluegill and green sunfishes		
Bluegills and bullheads*		
Bluegills and carp		
Bluegills and rough fish		
White and black crappie		
Carp and buffalo		

*Differences significant at the 95 per cent level of confidence.
**Differences significant at the 99 per cent level of confidence.

SUMMARY

Analyses of the standing crop estimates indicate:

1. No correlation between the area of a body of water and the weight of the fish crop per acre.

2. A negative regression of standing crop per acre on the maximum depth of the body of water.

3. A positive correlation between carbonate content of the water and the standing crop of fish per acre.

4. Greater standing crops for species with short food chains than for species with predatory food habits.

5. An increase in the standing crop of a body of water as the number of species of fish increases, but maximum crops of selected species in lakes or ponds with not more than one other species.

6. Tendencies for some species to have smaller standing crops in the presence of certain other species (competition) and larger standing crops in the presence of other species (protocooperation).

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A Statistical Examination of *Anisakis* Larvae (Nematoda) in Herring (*Clupea pallasi*) of the British Columbia Coast[1]

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ABSTRACT

The presence of larval *Anisakis* in British Columbia herring was examined during the winter fisheries of 1950–51 and 1951–52. In the commercial catches in the Strait of Georgia the incidence was found to be between 80 and 90%. In Hecate Strait, on the west coast of Vancouver Island and in the mainland coastal area of Queen Charlotte Sound it was between 90 and 100%. The intensity of infection varied greatly in different fishing areas (i.e. in different herring populations). Generally, the maximum level of infection occurred in the Queen Charlotte Sound coastal regions, and decreased both north and south of this area. Fish on the west coast of Vancouver Island were more heavily infected than those on the east coast (Strait of Georgia). The level of infection increased with age, I-year fish (i.e. fish in their first year of life) being uninfected. The intensity of infection remained constant throughout the winter for any particular age and area and was the same for both sexes. In most areas the level of infection was a little lower in 1951–52 than in 1950–51.

INTRODUCTION

Herring in British Columbia coastal waters are frequently infected with larval nematodes of the genus *Anisakis*. The larvae are found tightly coiled in lenticular cysts in the body cavity. The heaviest concentration of cysts occurs in the mesenteries in the vicinity of the posterior region of the intestine.

The species of *Anisakis* involved is uncertain but is probably *A. simplex* (Rudolphi, 1809), which, in the adult stage, has been found in whales (Margolis and Pike, 1955) and porpoises (Margolis, unpublished data) on this coast.

A survey of the incidence and intensity of infection in the herring was undertaken during the winters of 1950–51 and 1951–52, with a view to locating areas of least infection from which catches relatively free of nematodes might be obtained. The counts were made by various members of the herring investigation staff at the Pacific Biological Station, concurrently with the regular herring sampling program. The nematodes were counted in each of the first 10 fish of the samples taken for analysis of age composition, etc. (Tester and Stevenson, 1947). Fish whose age could not be determined from scale readings were not considered in the analysis. On the basis of length and weight, these fish did not seem to belong to any one age-group.

A I-year fish is here defined as one in its first year of life, a II-year fish is one in its second year, etc.

After determining the incidence of infection, a cursory examination of the data on intensity revealed that the level of infection was not homogeneous. The

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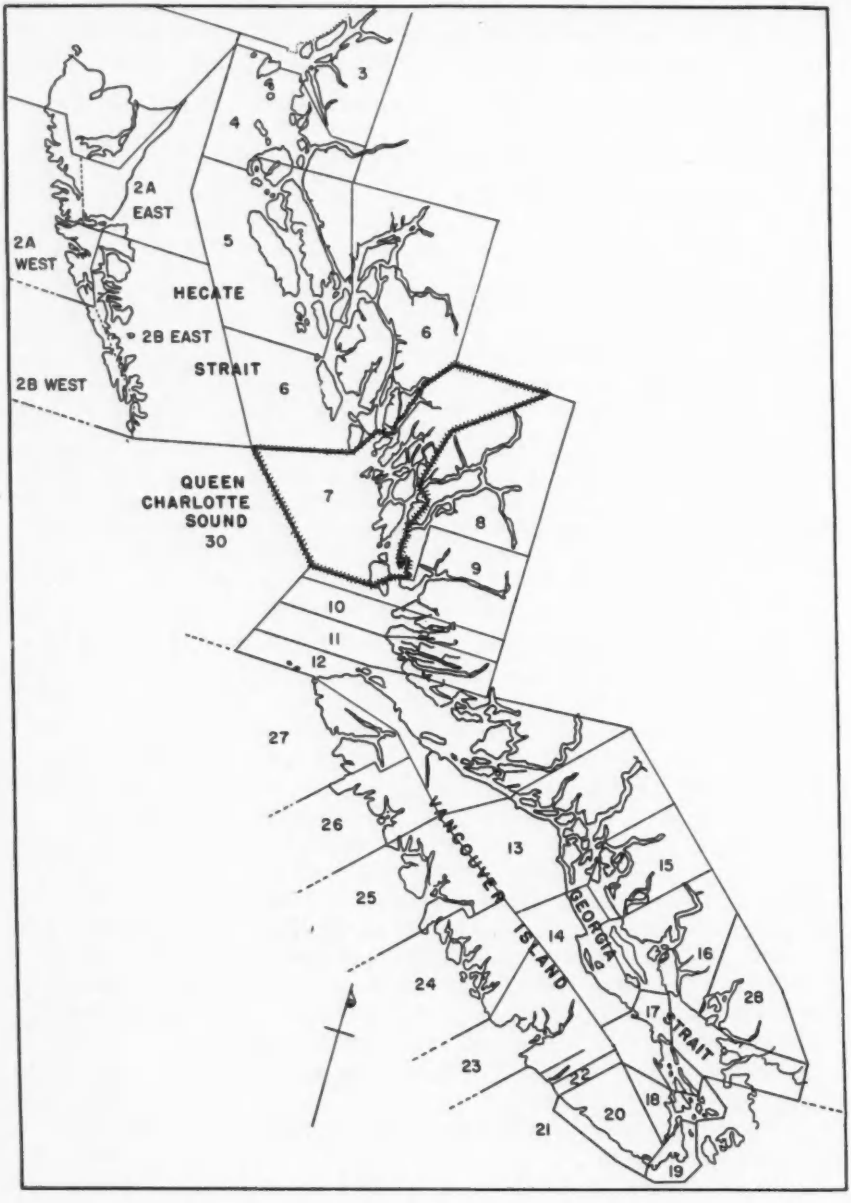


FIGURE 1. Map of British Columbia coast showing areas from which samples of herring were taken.

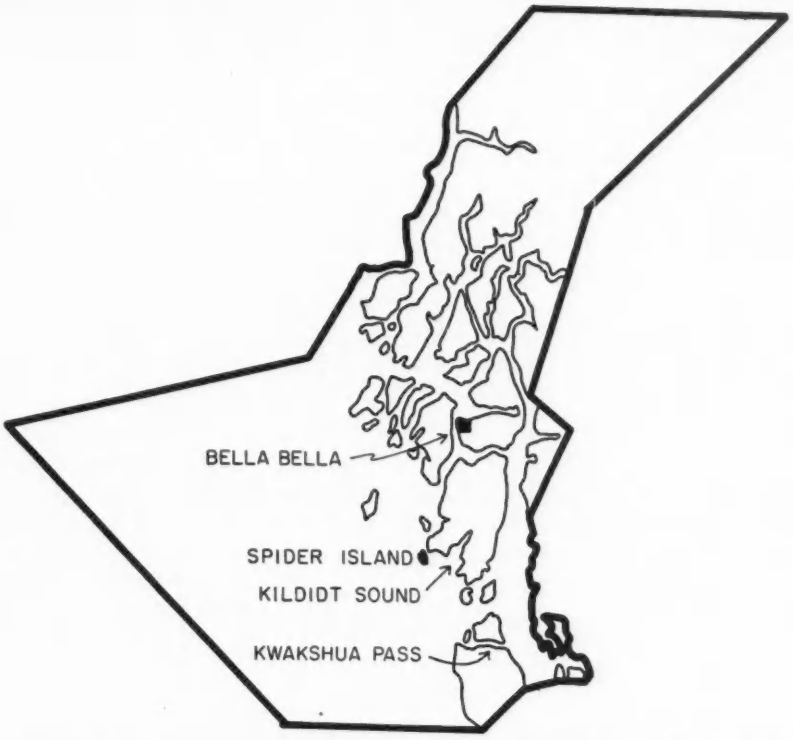


FIGURE 2. Map of area 7 showing particular localities from which samples were taken.

data were then analysed to determine what factors might be related to the level of infection.

Figure 1 is a map of the British Columbia coast, showing all fishing areas that were sampled. Figure 2 is an enlarged map of area 7.

INCIDENCE

The incidence of infected fish was determined as a percentage of the number of fish sampled. In 1950–51, 91.9% of 2,261 fish of the entire fishery were infected. In 1951–52 the incidence in 3,047 fish was 86.4%. Table I shows the incidence of infection in each age-group, of all sampled areas, for the two years. The major fishing areas can be divided into two groups on the basis of the incidence of nematode infection. In Hecate Strait (areas 2B(E), 5 and 6), the coastal region of Queen Charlotte Sound (area 7), and on the west coast of Vancouver Island (areas 23, 24 and 25) the incidence was between 90 and 100%. In the Strait of Georgia (areas 17A, 17B and 18), 80–90% of the fish were infected.

TABLE I. Percentage of infected fish in each age-group, for all areas, in 1950–51 and 1951–52 (1951–52 values in italics; number of fish samples in parentheses).

Area	Age I	II	III	IV	V	VI	VII+	Mean for all ages
2B (E)	...	...	100(16)	96.3(82)	96.3(27)	100(18)	100(9)	97.4(152)
	0.0(1)	*69.4(36)*	*93.3(45)*	*100(85)*	*100(52)*	*100(9)*	*100(1)*	*93.4(229)*
5	...	58.8(18)	94.3(87)	94.0(250)	100(50)	100(30)	94.1(16)	93.8(451)
	...	*56.0(25)*	*86.9(61)*	*98.3(240)*	*99.3(269)*	*100(37)*	*100(6)*	*96.1(638)*
6	*0.0(2)*	*77.6(28)*	*87.7(57)*	*100(56)*	*100(130)*	*100(14)*	*100(3)*	*94.8(290)*
7	...	37.5(8)	99.3(147)	99.6(284)	97.3(73)	100(32)	100(8)	98.3(552)
	0.0(6)	*75.0(8)*	*98.5(64)*	*99.0(96)*	*100(71)*	*100(10)*	*100(3)*	*96.2(258)*
9	...	*50.0(12)*	*20.0(5)*	*66.7(3)*	...	...	...	*45.0(20)*
12	*0.0(88)*	*14.0(56)*	*72.2(36)*	*91.9(37)*	*85.7(21)*	*80.0(10)*	*100(5)*	*39.0(253)*
13	...	37.5(8)	70.6(51)	79.0(81)	89.5(19)	100(7)	100(3)	76.9(169)
	...	*11.4(44)*	*72.6(68)*	*95.0(25)*	*83.3(12)*	*100(5)*	...	*59.7(154)*
17A	...	50.0(4)	88.9(99)	83.6(55)	90.9(11)	100(3)	100(1)	86.7(173)
	...	*50.0(4)*	*82.5(202)*	*95.0(99)*	*96.0(25)*	*100(7)*	...	*87.2(337)*
17B	...	33.3(3)	82.9(129)	91.1(45)	100(10)	...	...	85.0(187)
18	...	0.0(3)	84.9(146)	82.4(51)	100(9)	100(1)	...	83.8(210)
	...	*14.3(35)*	*88.1(226)*	*86.0(85)*	*96.9(31)*	*100(7)*	*100(1)*	*81.8(385)*
23	...	81.1(37)	98.0(152)	97.4(154)	100(21)	100(4)	...	96.2(368)
	...	*55.6(9)*	*96.7(91)*	*94.7(38)*	*100(19)*	*100(3)*	...	*94.4(160)*
24	...	...	*100(9)*	*100(1)*	...	...	...	*100(10)*
25	...	*100(2)*	*100(32)*	*100(93)*	*100(196)*	*100(28)*	*100(10)*	*100(361)*

INTENSITY

Preliminary analysis of the data did not show any differences between the sexes in the level of infection, or changes during the course of the fishery. The data for each year were then grouped by area and age of fish and the resulting frequency distributions of number of nematodes per fish examined.

The general form of the frequency distributions, which were skewed and had variances greater than their means, indicated that they would require transformation before any analytical methods appropriate for normal distributions could be used. On theoretical grounds the negative binomial distribution seemed likely, the frequencies being indicated by the expansion of:

$$(q - p)^{-k},$$

where $p = m/k$, $q = 1 + p$, and m is the arithmetic mean of the distribution. As a guide to an appropriate transformation, values of k were determined for three of the distributions (determination of a general value for the whole body of data would have involved excessive calculations).

Determination of k

The 1950–51 data were used and estimates of k were made for three groups. III-year and IV-year fish were chosen because these constituted a large proportion of the catch in any area and, unlike II-year fish, these ages would be nearly fully represented in the fishery. Areas were selected that would give samples that were sufficiently large but not unwieldy.

Estimates of k were first obtained by using the equation:

$$k = \frac{\bar{x}^2}{s^2 - \bar{x}},$$

where $\bar{x}$ is the mean of the distribution and s its standard deviation. Since in each case the efficiency of this estimate was less than 90%, it seemed as well to calculate the maximum likelihood estimate by Haldane's iterative method (Bliss and Fisher, 1953), using the above values as a starting point. The final values were found by graphical interpolation. The k-values obtained by this method are as follows, the initial trial estimate being in brackets:

(a) IV-year fish in area 5, $k = 1.26$ (1.11),

(b) III-year fish in area 7 (Kwakshua Pass), $k = 1.05$ (1.03),

(c) III-year fish in area 13, $k = 0.41$ (0.60).

As these values were all smaller than 2 a logarithmic transformation was indicated (Barnes, 1952); the one chosen was:

$$y = 100 \log (x + 1),$$

as 1 was the smallest constant that did not give negative values. Logarithms were taken to two places, and the factor 100 was introduced merely to eliminate the decimal point from tables and computations.

The effectiveness of this transformation in stabilizing the variance is shown in Table II. In Figure 3 an example of the frequency distribution is given. In all the following tables and discussion the values quoted are transformed values unless otherwise stated.

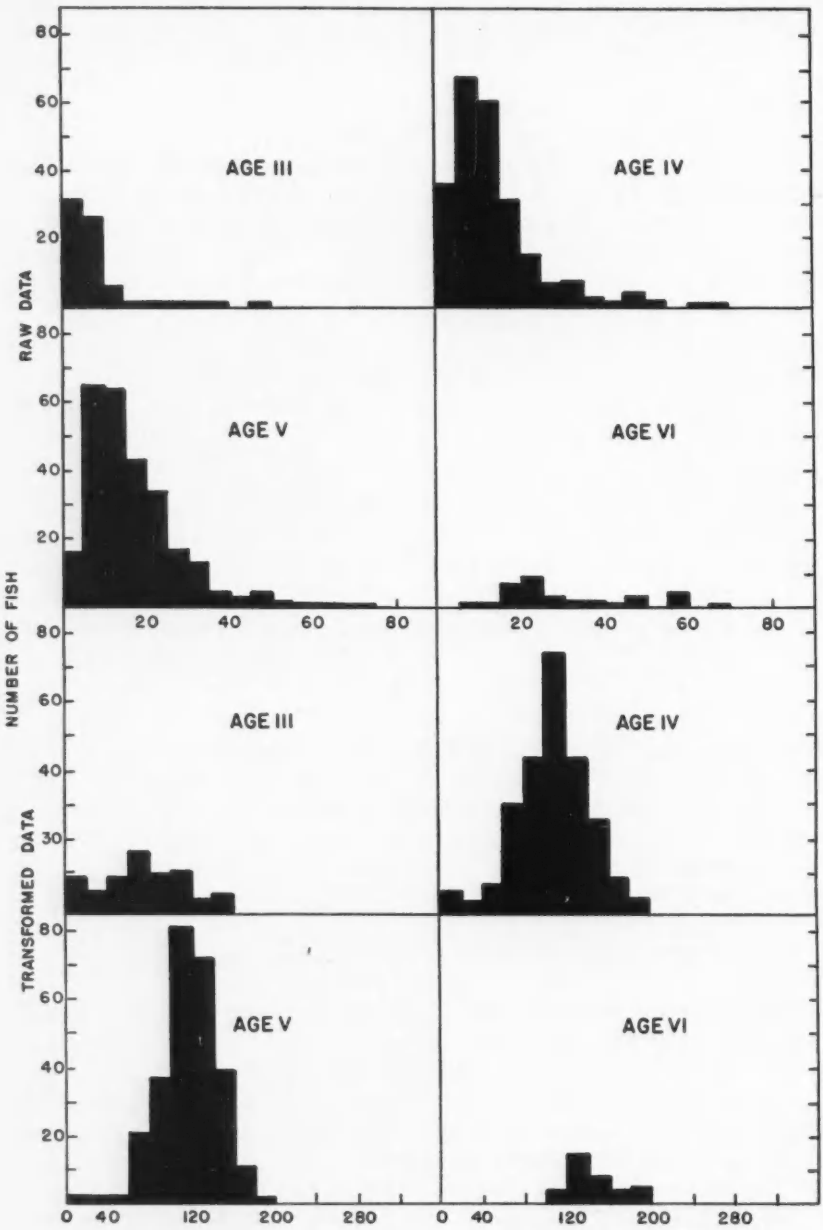


FIGURE 3. Frequency distributions for area 5, 1951–52, showing the effect of logarithmic transformation. Top four panels: actual numbers of nematodes. Bottom four panels: frequencies on the transformed scale.

TABLE II. Effect of transformation: $y = 100 \log_{10}(x+1)$. Area 13, 1950–51.

	II	III	IV	V	VI	VII+
RAW DATA						
Mean	2.88	5.94	9.28	16.95	16.29	20.33
s^2	38.71	70.66	175.30	571.50	189.50	274.50
TRANSFORMED						
Mean	29.50	55.73	72.91	91.21	106.00	117.67
s^2	2,189	2,506	2,634	3,539	1,936	2,605

DIFFERENCE WITH SEX

Although when determining the appropriate transformation, differences in sex were ignored as being unlikely to affect the general distribution, this aspect was examined more closely before proceeding further. Area 5 was selected and *t*-tests performed on male and female transformed distributions for each age-group. In every case the P value was greater than 0.2; thus there was no indication that male and female did not belong to the same population (Table III). The conclusion that the sexes were similarly infected was expected from a cursory examination, as the slightly greater mean rate of infection shown by III-year and older males in this area was not apparent in other areas. Males and females were not separated in subsequent analysis.

TABLE III. Comparison of infection of each sex in area 5, 1950–51.

Age	Mean no. of nematodes (transformed scale)		Difference	t	D.F.	P
	Male	Female				
II	119.63	121.50	−1.87	0.0519	12	>0.5
III	175.39	169.24	+6.15	0.2197	86	>0.5
IV	193.67	187.37	+6.30	1.0981	239	>0.2
V	215.00	209.21	+5.79	0.5052	49	>0.5
VI	239.00	224.89	+14.11	0.9864	28	>0.3
VII+	243.67	219.91	+23.76	0.9859	15	>0.3

DIFFERENCE WITH TIME OF YEAR

The samples available were taken over the period extending from October to March, although no one area was sampled throughout this interval. The samples for 1951–52 were grouped in 10-day periods and their distribution between October and March was examined (Table IV). Area 5 was selected as being sampled over the longest time interval and differences between 10-day periods in this area were examined for both years. The means for each age-group for each period were determined (Table V) and the variance analysed (Table VI). Each age-group was considered separately and the P from the F-value was not in any case less than 0.05, except for age-group III in 1950–51, when it lay between 0.05 and 0.01. It seems likely that this variation is attributable to

TABLE IV. Number of samples examined in each period (10 fish in each sample), 1951–52.

		2B(E)	5	6	7	9	12	13	17A	17B	18	23	24	25
Oct.	11–20								2					
	21–31													
Nov.	1–10								2					
	11–20							12	30					
	21–30		2			2		4	1		19			
Dec.	1–10		17								14	9		
	11–20		22								7		1	
	21–31													
Jan.	1–10				12		4					4		
	11–20		26	14	5		5					3		
	21–31			6	7		10							
Feb.	1–10			10	3									10
	11–20	5												27
	21–28	2												
Mar.	1–10	16												

TABLE V. Mean levels of infection (in transformed scale) for the years 1950–51 and 1951–52 in area 5 (1951–52 values in italics).

	II	III	IV	V	VI	VII+	Total	No. of fish
Nov. 21–31	...	*60.0*	*102.0*	*113.3*	*136.5*	...	*111.1*	18
Dec. 1–10	7.5	58.7	89.5	130.7	123.0	156.7	84.7	83
	18.6	*67.7*	*97.7*	*110.5*	*134.0*	*142.0*	*97.0*	165
Dec. 11–20	53.2	83.8	89.7	107.0	132.7	114.3	92.4	229
	29.0	*64.3*	*108.1*	*115.1*	*142.2*	*169.0*	*108.8*	210
Jan. 1–10	...	76.1	97.4	122.2	120.5	141.5	101.9	86
Jan. 11–20	78	100.1	107.9	108.7	154.8	150.7	112.3	53
	37.0	*75.4*	*108.2*	*121.8*	*151.5*	*202*	*110.4*	245
Total	44.4	78.3	93.5	114.4	132.9	139.3	95.2	
	28.0	*69.7*	*105.6*	*116.0*	*144.0*	*181.0*	*106.5*	

sampling fluctuation rather than indicating a real difference, particularly as the mean values for this age do not show any continuous trend (58.7, 83.8, 76.1, 100.1).

The significant differences between the overall values for all age-groups must be attributable to differences in age-composition. As the infection seemed to increase with time, during the 1950–51 fishery, the age-composition of the sample was investigated (Table VII). There was a decline in the numbers of II-year fish, a decline that was also reflected in the age-composition of the larger samples from which the nematode samples were taken. This decline did not occur during the 1951–52 fishery but the mean age of the population was nevertheless greater because the V-year fish were predominant, whereas in 1950–51 the same year class was the strongest one, as IV-year fish. The lesser abundance of IV-year fish seems to be associated with a high rate of infection (Fig. 9) but it is not possible to trace such an association in other areas.

It was concluded that differences within a season in the level of infection of a particular age-group were not significant, even where the age-composition of the area was changing. Subsequent comparison of areas confirmed this opinion: areas 17A and 18 in 1951–52, for instance, were found not to differ significantly although fished during consecutive months. Biologically, these results are to be expected, since infection is by ingestion and herring do not feed much during the winter months.

COMPARISON OF AREAS

The age-composition of the eight areas sampled in 1950–51 was found to differ significantly between areas, so an approximate analysis of variance over the whole fishery was not attempted. To distinguish differences between fish of a given age in different areas it was necessary to compare each age-group separately. Nevertheless, in most instances initial comparisons were made by taking all ages together; where differences were found, age-groups were then compared separately to determine whether the differences were due to age-composition or level

TABLE VI. Variation in level of infection over 10-day periods in area 5. (One asterisk indicates an F-value significant at the P=0.05 level; two asterisks, the P=0.01 level.)

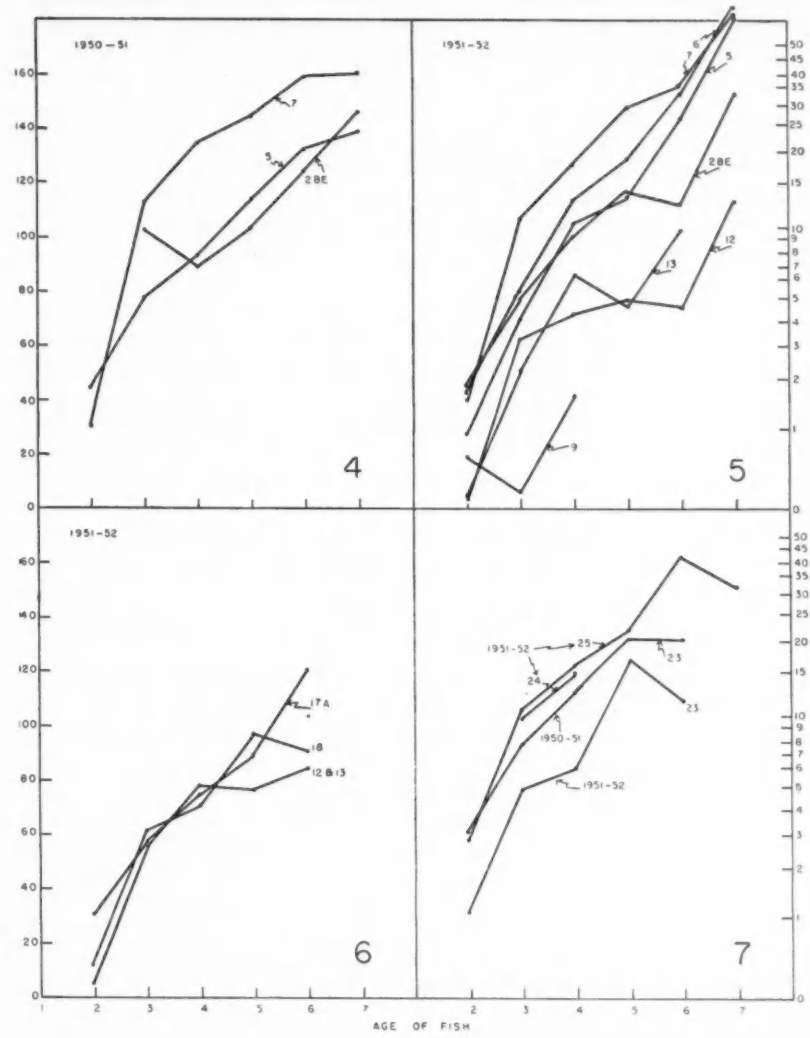
Age	Source	1950–51				1951–52			
		Sum of squares	D.F.	Mean square	F-value	Sum of squares	D.F.	Mean square	F-value
II	Total	45,458	17			20,471	24		
	Periods	7,571	2	3,786	1.50	1,699	2	850	<1
	Residual	37,887	15	2,525		18,772	22	853	
III	Total	105,213	86			101,667	60		
	Periods	11,698	3	3,899	3.46*	1,491	3	497	<1
	Residual	93,515	83	1,127		100,176	57	1,757	
IV	Total	394,729	249			257,214	239		
	Periods	10,517	3	3,506	2.24	4,729	3	1,576	1.47
	Residual	383,212	246	1,562		252,485	236	1,070	
V	Total	66,771	49			211,554	268		
	Periods	4,076	3	1,359	1.00	5,482	3	1,827	2.35
	Residual	62,695	46	1,363		206,072	265	778	
VI	Total	44,396	29			19,334	36		
	Periods	2,931	3	977	<1	1,398	3	466	<1
	Residual	41,465	26	1,595		17,936	33	544	
VII	Total	8,833	15			6,224	5		
	Periods	3,830	3	1,277	3.06	3,132	2	1,566	1.52
	Residual	5,003	12	417		3,092	3	1,031	
All	Total	829,520	450			962,982	627		
	Periods	30,274	3	10,091	5.64**	20,123	3	6,708	4.51**
	Residual	799,246	447	1,788		942,859	634	1,487	

TABLE VII. Percentage age distribution over periods sampled in area 5.

	Total sample							Sub-sample						
	II	III	IV	V	VI	VII+	Mean age	II	III	IV	V	VI	VII+	Mean age
1950-51														
Dec. 1–10	9	22	54	9	5	1	3.82	5	22	61	7	1	4	3.89
Dec. 11–20	4	18	59	10	6	2	4.02	6	19	54	11	8	2	4.03
Jan. 1–10	3	18	58	11	7	5	4.16	0	21	48	17	7	7	4.31
Jan. 11–20	1	13	64	12	5	5	4.22	2	13	66	6	8	6	4.22
1951-52														
Nov. 21–30	4	5	25	58	7	2	4.64	0	6	17	67	11	0	4.83
Dec. 1–10	4	10	34	46	5	1	4.41	6	10	35	46	3	1	+.31
Dec. 11–20	7	10	33	43	6	1	4.34	2	9	37	43	8	1	4.49
Jan. 11–20	4	10	34	44	7	1	4.43	4	10	42	37	5	1	4.33

TABLE VIII. Mean level of infection (in actual number of nematodes) for each area and age for 1950–51 and 1951–52. (Numbers of fish are in parentheses; 1951–52 values in italics.)

Area	Age I	II	III	IV	V	VI	VII+	All ages
2B(E)	...	...	14.2(16)	10.1(82)	15.1(27)	26.2(18)	37.2(9)	14.8(152)
	0(1)	*5.1(36)*	*7.2(45)*	*11.4(85)*	*17.0(52)*	*15.9(9)*	*33.0(1)*	*11.1(229)*
5	...	5.6(18)	7.0(87)	11.7(250)	17.7(50)	28.2(30)	25.5(16)	12.8(451)
	...	*1.4(25)*	*6.8(61)*	*13.7(240)*	*16.8(259)*	*30.9(37)*	*85.3(6)*	*15.5(639)*
6	*0(2)*	*2.4(28)*	*7.0(57)*	*14.7(56)*	*24.5(130)*	*35.2(14)*	*72.3(3)*	*17.9(290)*
7	...	2.9(8)	18.2(147)	27.7(284)	36.7(73)	46.2(32)	42.4(8)	27.3(552)
	0(6)	*2.0(8)*	*14.9(64)*	*24.7(96)*	*33.9(71)*	*40.9(10)*	*69.3(3)*	*24.4(258)*
9	...	*0.8(12)*	*0.2(5)*	*2.3(3)*	...	...	...	*0.8(20)*
12	*0(88)*	*0.3(56)*	*7.9(36)*	*6.1(36)*	*6.7(21)*	*10.4(10)*	*16.8(5)*	*3.4(253)*
13	...	2.9(8)	6.2(51)	9.5(81)	16.9(19)	16.3(7)	20.3(3)	9.5(169)
	...	*0.2(44)*	*4.4(68)*	*10.1(25)*	*10.1(12)*	*16.4(5)*	...	*5.0(154)*
17A	...	1.3(4)	4.3(99)	7.7(55)	8.0(11)	12.3(3)	7.0(1)	5.7(173)
	...	*2.3(4)*	*4.0(202)*	*7.0(99)*	*8.8(25)*	*17.1(7)*	...	*5.5(337)*
17B	...	3.3(3)	5.3(129)	11.0(45)	12.0(10)	...	...	7.0(187)
18	...	0.0(3)	5.5(146)	6.9(51)	13.9(9)	4(1)	...	6.1(210)
	...	*1.0(35)*	*4.3(226)*	*6.6(85)*	*10.6(31)*	*9.7(7)*	*8.0(1)*	*5.2(385)*
23	...	5.0(37)	10.0(152)	15.8(154)	24.6(21)	29.8(4)	...	12.9(368)
	...	*1.7(9)*	*6.1(91)*	*8.7(38)*	*20.1(19)*	*14.3(3)*	...	*8.3(160)*
24	...	...	*14.2(9)*	*15.0(1)*	...	...	...	*14.3(10)*
25	...	*3.0(2)*	*13.0(32)*	*19.0(93)*	*25.6(196)*	*47.3(28)*	*36.5(10)*	*24.6(361)*



FIGURES 4–7. Relation of mean level of infection to age, in the areas and years indicated. The scales on both sides apply to all figures: **4.** Areas 2B(E), 5 and 7 during 1950–51. **5.** Areas 2B(E), 5, 6 and 7, also 9, 12 and 13 during 1951–52. **6.** Areas 12 and 13 combined, 17A and 18 during 1951–52. **7.** Area 23 during 1950–51 and areas 23, 24 and 25 during 1951–52. The right-hand ordinate scale shows the actual number of nematodes per fish; the left-hand scale is on the transformed basis.

of infection. Although the frequency distributions for the areas taken as a whole will not be normal, particularly where the lower age-groups predominate, this method was considered sufficiently accurate, as computation of F-values has been shown to be valid with moderately skewed distributions. Where a comparison of areas as a whole has not shown any significant difference between the general means there has been close agreement between the means for each age-group (Table VIII and Fig. 4–7). As similarly infected fish are likely to come from adjacent areas, a formal method of comparing individual means was considered too lengthy. Instead, once it was established that all the areas together differed significantly for fish of each age-group, likely combinations of areas were determined by inspection and then tested (Table IX).

For the 1950–51 fishery the removal of area 7, the most highly infected area, did not leave a homogeneous population when all ages together or the well-represented age-group III were considered; further division into groups of areas was tried.

The three most northerly areas along the coast, 5, 7 and 13 were not homogeneous but the more southerly areas, 13, 17A, 17B and 18, were found to have mean rates of infection that could have come from the same population.

For the second year the most northerly areas, 5, 6 and 2B(E), were compared. Although when taking overall values areas 5 and 6 were found not to differ significantly from each other, but to differ from 2B(E), comparison of individual age-groups modifies this conclusion. All three areas are similarly infected at ages II, III and IV, but area 6 shows significantly high infection at age V and area 2B(E) shows low infection at age VI (Fig. 5).

These two exceptional values needed further consideration. The low value for area 2B(E) is based on only nine fish, and as it is lower than that for V-year fish in the area, it is concluded that this is a freak value and that there is likely no real difference between the level of infection at a given age in areas 5 and 2B(E). This is confirmed by comparing the same areas in the previous year; the overall value for ages above III (there were no II-year-olds in 2B(E)) does not differ significantly for the two areas. The other significantly different mean, the high value for V-year fish in area 6, seems however to reflect a real difference, as area 6 has higher values than the other two areas for all fish of age III or more.

The general mean level of infection of area 7 is higher than that of any other area in each year, except for area 25, 1951–52. This apparent similarity in level of infection is due to differences in age-composition. Actually, area 7 is more highly infected than area 25 for ages III-V, which constitute almost 90% of the samples. It is more highly infected than area 5 for all ages beyond II in the first year (Fig. 4) and more highly infected than areas 5 or 6 for ages III to VI inclusive in the second year. It seems reasonable to conclude that areas 5, 6 and 7 show a progressive increase towards the south in their level of infection.

Proceeding further south, area 9 is only represented by 20 fish; these are all young and have comparatively few nematodes. The next two areas, 12 and 13, are less heavily infected than areas 5, 2B(E), 6 and 7. During the 1951–52 season they did not show any significant differences when each age-group was

TABLE IX. Tests of differences in level of infection between areas, by analysis of variance. (Significance of asterisks as in Table VI.)

Areas	Ages	Degrees of freedom n_1	Degrees of freedom n_2	F-value
1950–51				
All	All	7	2,255	101.07**
	III	7	820	32.86**
	IV	7	993	53.99**
	V	7	212	9.61**
	VI	6	88	4.63**
	VII+	4	32	3.88**
All except 7	All	6	1,704	34.26**
	III	6	674	15.18**
17A, 17B, 18	All	2	567	0.51
5, 7, 13	All	2	1,170	166.74**
17A, 17B, 18, 13	All	3	735	0.29
1951–52				
All	All	11	3,084	163**
	II	10	248	6.77
	III	11	884	17.38**
	IV	11	847	24.02**
	V	9	816	28.51**
	VI	9	120	108**
2B(E), 5	All	1	583	1.16
5, 6	All	1	927	0.17
5, 6, 7	All	2	1,184	10.89**
5, 6, 2B(E)	All	2	1,155	11.76**
	All but VI and VII	2	1,084	9.15**
	III	2	160	0.71
	IV	2	378	2.86
	V	2	448	7.88**
	VI	2	57	8.24**
5, 6	VI	1	49	1.44
5, 6, 7	III	2	179	17.37**
9, 12	II	1	66	9.21**
	III	1	39	5.60*
	IV	1	38	2.07
12, 13	II	1	98	0.03
	III	1	102	3.72
	IV	1	60	2.58
	V	1	31	0.00
	VI	1	13	1.12
17, 18	All	1	720	1.87
17, 18, 13	All	2	873	12.68**
12, 13, 17A, 18	II	3	135	3.55**
	III	3	529	2.51
	IV	3	242	1.41
	V	3	85	1.72
	VI	3	24	1.58
24, 25	III and IV	1	133	1.95
23, 25	All	1	519	276.80**
	III	1	121	24.65**

compared, although different age-composition gave a lower overall value in area 12. Going further south still and considering areas 17B and 18 as well as 12 and 13, no significant difference is found at any age apart from a high infection of II-year fish in area 17B (Fig. 6).

In the first year only area 23 was sampled on the west coast of Vancouver Island; in the second year areas 23, 24 and 25 were sampled. In the small sample from area 24 only age-groups III and IV were represented and their infection did not differ from that of area 25. The infection of area 23 was significantly less, being lower for each age-group than area 25. It was higher than that of the areas on the east coast of Vancouver Island.

It was concluded that areas 5 and 2B(E) were similarly infected and that areas 6 and 7 were progressively more highly infected. The areas on the east coast of Vancouver Island all showed about the same level of infection, which was lower than that found in the more northerly areas, or on the west coast of Vancouver Island. On the west coast the lowest level of infection was in the Barkley Sound region, being greater in areas farther north.

Subdivision of Area 7

It was possible to subdivide area 7 into the four areas, Kwakshua Pass, Kildidt Sound, Bellabella and Spider Island (Fig. 2). This was done with the 1950–51 data, the number of fish of known age in each area being 321, 183, 39 and 9, respectively. The age-composition of the four sub-areas was tested and the χ^2 value found to be 14.893 with 15 degrees of freedom. The probability of a larger value was between 0.50 and 0.30, indicating that the four sub-areas could be supporting a homogeneous population. As the similarity of age-composition was thus established, it was considered sufficiently accurate to compare the total means. These did not differ significantly (Table X).

Comparison of Years

For a comparison of the level of infection in the two years, those areas which were duplicated were selected. This included seven out of the eight areas for which data were available in 1950–51. When all the areas were considered together the 1951–52 fish were found to be less heavily infected than those of the previous year in each age-group up to VI, the difference being significant for age-groups IV and younger (Fig. 14, Table XI). When the areas are considered separately however, some exceptions are found. The infection in the second year in area 2B(E) is greater (0.05 level) for IV-year fish, which constitute the bulk of the catch, although it is less for III-year fish (0.05 level). This increase in the level of infection also appears in area 5 for all IV-year fish and older (significant for V- and VI- and highly significant for IV- and VII-year fish), but there is a highly significant decrease in the level among the younger age-groups. Apart from the older fish of these two areas, which are the most northerly of those sampled and do not differ significantly from each other in either year, the level of infection is lower for the second year in all cases where there is a significant difference for all fish up to VI-year inclusive. Of VII-year fish and older only 37

TABLE X. Mean number of nematodes (in transformed scale) and analysis of variance for subdivisions of area 7, 1950–51. (Numbers of fish in parentheses.)

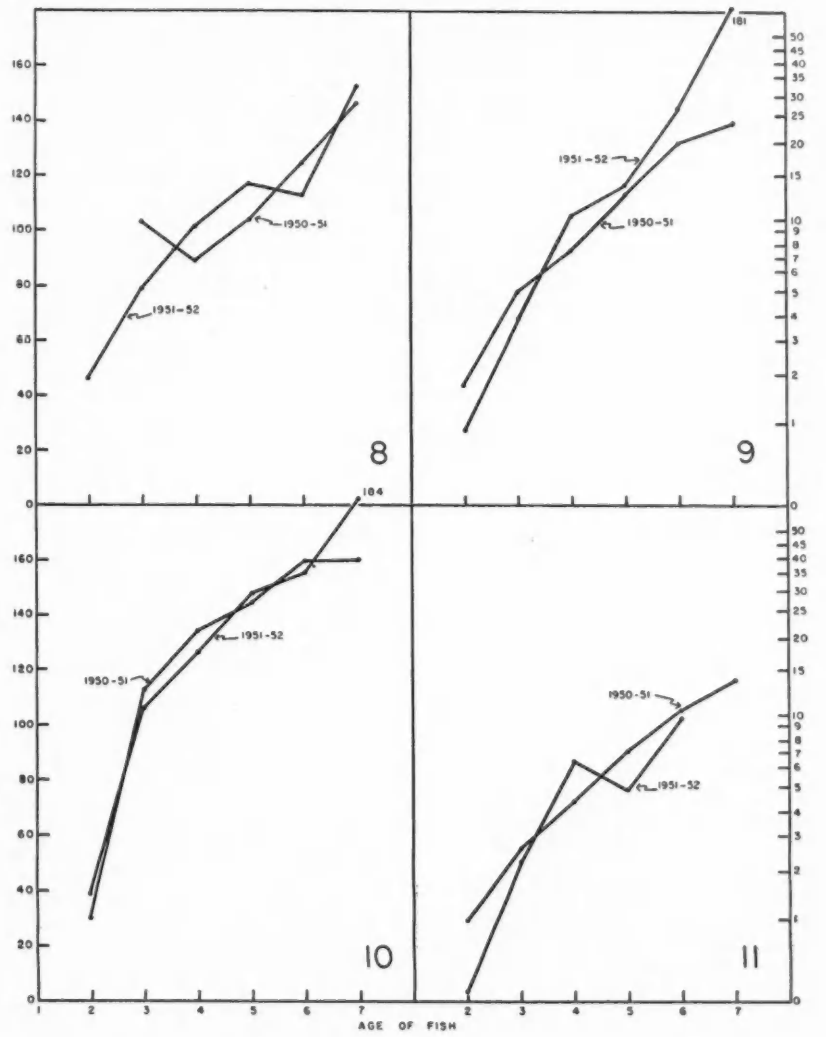
	Age						
	II	III	IV	V	VI	VII	All ages
Area 7							
Kwakshua Pass	30.3 (8)	110.6 (79)	131.5 (163)	140.4 (48)	163.2 (19)	170.3 (4)	127.5 (321)
Kildidt Sound		116.1 (59)	141.7 (94)	155.4 (19)	163.6 (8)	153.0 (3)	136.0 (183)
Bella Bella		118.3 (7)	140.6 (22)	157.0 (5)	140.8 (4)	149.0 (1)	138.9 (39)
Spider Island		130.5 (2)	114.0 (5)	132.0 (1)	145.0 (1)		123.1 (9)

Source of variation	Sum of squares	Degrees of freedom	Mean square	Significance
Total	824,450	551		
Areas	11,431	3	3810	F = 2.5
Residual	813,019	549	1481	not significant

TABLE XI. Tests of differences in level of infection between the years 1950–51 and 1951–52, by analysis of variance. (Significance of asterisks as in Table VI.)

Areas	Ages	Degrees of freedom n_1	Degrees of freedom n_2	F-value	Year of heavier infection
All	All	1	5357	32.34**	1950–51
	II	1	337	24.53**	1950–51
	III	1	1722	36.37**	1950–51
	IV	1	1858	4.36*	1950–51
	V	1	1045	1.14	...
	VI	1	223	0.10	...
	VII	1	65	3.31	...
23	All	1	526	29.27**	1950–51
	II	1	44	3.99	...
	III	1	241	20.50**	1950–51
	IV	1	190	24.75**	1950–51
	V	1	38	0.69	...
	VI	1	5	0.51	...
17, 18 of 1951–52 and 17A, 17B, 18, 13 of 1950–51	All	5	1355	1.39	...
17A and 18	II	3	42	0.82	...
	III	3	669	2.27	...
	IV	3	286	0.50	...
	V	3	72	1.36	...
	VI	3	14	1.11	...
2B(E), 5, 7, 13 17A, 18, 23	All	1	4234	71.16**	1950–51
	II	1	237	19.18**	1950–51
	III	1	1453	66.73**	1950–51
	IV	1	1623	10.05**	1950–51
	V	1	687	1.04	...
	VI	1	171	0.97	...
	VII	1	46	6.60**	1951–52
2B(E)	All	1	380	151.32**	1950–51
	III	1	59	5.69*	1950–51
	IV	1	165	5.24*	1951–52
	V	1	77	2.73	...
	VI	1	25	0.60	...
5	All	1	1087	20.50**	1951–52
	II	1	41	8.74**	1950–51
	III	1	146	11.94**	1950–51
	IV	1	488	25.49**	1951–52
	V	1	317	5.14*	1951–52
	VI	1	65	6.99*	1951–52
	VII	1	20	35.97**	1951–52
7	All	1	808	5.16*	1950–51
	II	1	14	0.33	...
	III	1	209	1.21	...
	IV	1	378	3.99*	1950–51
	V	1	142	0.22	...
	VI	1	40	0.13	...
13	All	1	321	15.61**	1950–51
	II	1	50	9.89**	1950–51
	III	1	117	0.29**	...
	IV	1	104	1.67	...
	V	1	29	0.49	...
	VI	1	10	0.06	...

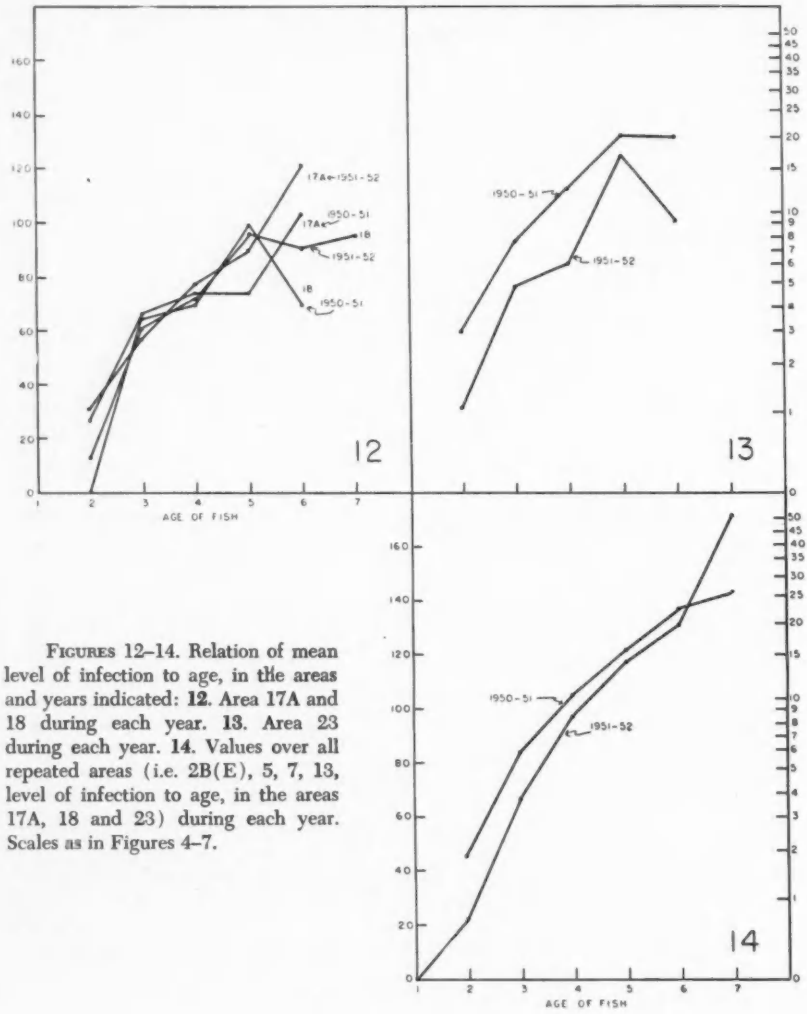
were sampled in the first year and 11 in the second, and area 5 was the only area where five or more were sampled in each year. With such small samples the higher overall rate of infection in 1951–52, though formally significant, cannot be considered as necessarily representative of the population.



FIGURES 8–11. Relation of mean level of infection to age, in the areas and years indicated: **8.** Area 2B(E) during each year. **9.** Area 5 during each year. **10.** Area 7 during each year. **11.** Area 13 during each year. Scales as in Figures 4–7.

The pairs of curves describing the mean number of nematodes for fish of each age-group are shown in Figures 8–13. The related age–composition curves for each of these were also drawn and examined. There did not generally appear to be any relation between the abundance of an age-group and its level of infection, either at the time considered or in the following year. Nor was there any indication of an interaction between age and frequency of nematodes, although this was not tested analytically.

As it is believed that the nematodes remain in the fish for several years the



FIGURES 12–14. Relation of mean level of infection to age, in the areas and years indicated: **12.** Area 17A and 18 during each year. **13.** Area 23 during each year. **14.** Values over all repeated areas (i.e. 2B(E), 5, 7, 13, level of infection to age, in the areas 17A, 18 and 23) during each year. Scales as in Figures 4–7.

curves were examined to see whether a highly infected age-group can be followed from year to year. In area 7 a high rate of infection among the IV-year fish in 1950–51 is followed by a high rate among V-year fish in the following year, but similar repetition is not apparent in other areas. It would not be expected in those areas where the samples are so small that random fluctuations would obscure any real preference for a particular year-class, but might have been found in area 5 if this area consisted of the same population in both years.

Increase with Age

Throughout the data the increase in the number of nematodes with increase in age is quite apparent. Although the means for individual areas show irregularities, they all show the same general trend (Fig. 4–13), even those areas which are less heavily infected. In Figure 14 the irregularities have become smoothed and the yearly trends are apparent. The lower overall values for the second year still show large annual increments for each year-class.

Before the antilogarithms of these transformed means can be found each must be multiplied by 1.15 times its variance (Barnes, 1952). Changed back

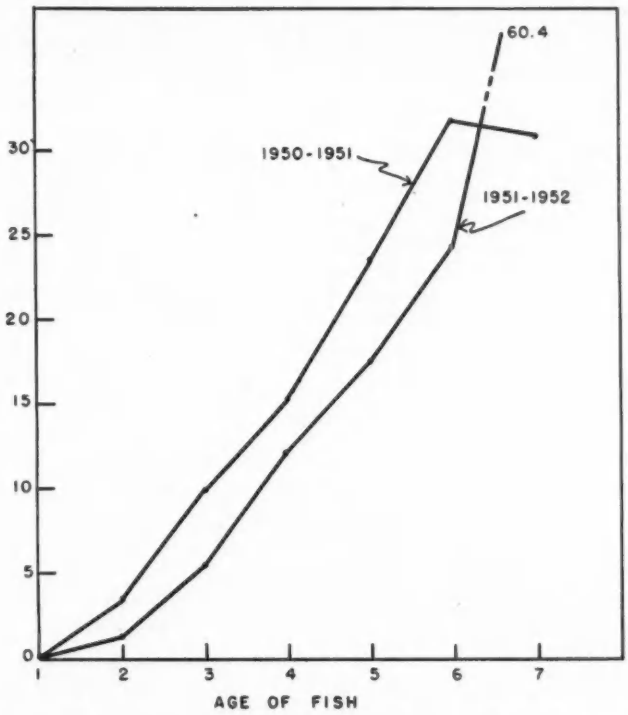


Figure 15. Untransformed values over all repeated areas during each year.
The ordinate scale indicates approximately the geometric mean number of nematodes per fish.

to the original scale, the means for the duplicated areas show that not only do the mean numbers of nematodes increase with increased age of the fish, but the increments between those successive age-groups also increased (Fig. 15).

I-year fish are uninfected. This is probably related to the inshore feeding habits and different diet of these fish as compared to older fish. I-year fish are lightly represented in the commercial herring fishery and hence only a comparatively small number (except for area 12) were examined from commercial catches (Tables I). However, about 200 I-year herring from different parts of the coast, collected for studies on growth, etc., were examined and found to be free of *Anisakis*.

The increase in numbers of nematodes per fish with increased age is probably attributable to their accumulation from year to year. The life span of the *Anisakis* larvae in herring is unknown.

ACKNOWLEDGMENTS

The authors wish to thank the many staff members working with herring who carried out the protracted task of counting the nematodes. Without their assistance this work would have been impossible. Thanks are also extended to Dr. W. E. Ricker for his advice on the statistical methods employed. The figures have been drawn by Mr. D. G. D. Denbigh.

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The Chaetognaths of Western Canadian Coastal Waters[1,2]

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ABSTRACT

Four species of chaetognaths were found in samples from 11 representative areas along the coastline of western Canada. *Sagitta elegans* was the most abundant and widely distributed species, occurring, at least in small numbers, in all the areas sampled. It was characteristic of the mixed coastal waters over the continental shelf and of the inland waters. *Eukrohnia hamata*, an oceanic form, occurred in most regions in small numbers as an immigrant, and was abundant toward the edge of the continental shelf. *Sagitta lyra*, strictly a deep sea species, was found only in the open waters along the outer coasts, and a few specimens of *Sagitta decipiens*, another oceanic form, were also taken in deep hauls from areas exposed to open ocean influence. The outer limit of *Sagitta elegans* corresponded with the inner limits of all three oceanic forms, though *Eukrohnia hamata* invaded the inland waters to some extent.

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INTRODUCTION

Chaetognaths, or arrow worms, are conspicuous members of the plankton communities of the oceans of the world. Moreover in some localities they have been found to be important indicator organisms, certain species being confined to

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waters with characteristic properties. When the requirements of various species are known, it may be possible to predict the character and origin of a water mass on the basis of the presence therein of a particular species of chaetognath. In the English Channel, for example, where two species are predominant, the abundance of either one of the species gives information concerning the source of that particular water, and this knowledge is of value to the herring industry (Kemp, 1938).

While chaetognaths have been or are being studied extensively in other parts of the world, including the east coast of Canada (Huntsman, 1919), very little is known about the species present off the west coast of Canada or about their distribution. Except for the work of Michael (1909–1919) in the San Diego region of California, there are no comprehensive studies of chaetognaths for any area in the eastern Pacific. Therefore, the present study was undertaken to acquire information about the chaetognath fauna of the coastal waters of Canada's western province of British Columbia. It was hoped that the distribution study would correlate with fundamental oceanographic data, and perhaps form a basis for more extensive plankton studies.

HISTORICAL

The most important taxonomic contributions on the chaetognaths were made in 1911 by Ritter-Zahony, whose careful and complete descriptions and good drawings have been the basis for all work on identification since that time. Also important were the contemporary works of Michael (1909, 1911) for the San Diego region. Thomson (1947) in Australia has brought up to date all the information on classification, technique, synonymy and distribution, and he has produced an excellent key for all valid species besides compiling an extensive bibliography. According to Thomson, there are now ten genera of chaetognaths, including one fossil form. Seven of these genera are monospecific; in one genus there are two species; in another three; and the genus *Sagitta* contains 26 valid species. Several forms that have been described are still considered doubtful species, and further investigation will be required, especially as to the environmental influence on the characteristics used for classification.

ZOOGEOGRAPHICAL DISTRIBUTION

While chaetognaths occur in all oceans, the individual species are restricted to different regions, some being deep sea forms, others living in the epiplankton of the open sea, and some inhabiting only the mixed waters over the continental shelves. None of the species is completely cosmopolitan, though many have a very wide distribution. Thomson (1947) states that eight of the Indo-Pacific forms do not reach the Atlantic, while five Atlantic species have not been reported from the Indo-Pacific. Species of deep oceanic waters have a wider distribution than those dwelling near the surface, since they are subject to very little temperature change. However, in the warmer parts of the world the oceanic species are found at greater depths than they are in the colder regions. Also, the immature

stages are often nearer the surface, while the mature ones are in deeper water. Thomson says that the bulk of the chaetognath population, as with the plankton in general, is concentrated in the upper 100 meters. Some of the species live at much greater depths, however, and it is possible that they could be taken in deeper hauls than are ordinarily made. Fraser (1949) states that one specimen of *Krohnitta subtalis* (Grassi) was taken where the depth exceeded 1,800 meters.

In a regional study, one must be aware of the fact that the chaetognath population may vary with the season, from one year to another, or with shifts in the currents. Some intensive regional studies have been undertaken, but much of the information available at present has been obtained through examination of material collected on occasional expeditions. As more regions are thoroughly studied, it will be possible to form a much better picture of the global distribution of the chaetognaths.

OCEANOGRAPHIC FACTORS INFLUENCING OCCURRENCE IN BRITISH COLUMBIA

In the north Pacific Ocean, the chaetognath fauna has been investigated in the Philippines (Michael, 1919), in Japan (Tokioka, 1940), and in southern California off San Diego (Michael, 1909, 1911). Species found in any of these regions could possibly occur also in British Columbia waters.

The North Equatorial Current flowing past the Philippines becomes the Kuroshio Current along the south and east of Japan. Here it is joined by cold waters from the north and continues eastward across the Pacific, approaching the coast of America in the vicinity of Vancouver Island. About 400 miles offshore it divides, part turning north and the remainder south (Tully, 1953). The British Columbia coast lies along the base of the triangle formed by these divergent streams. The northern branch, the Alaskan gyral, closely approaches the shore in the region of the northern Queen Charlotte Islands and Dixon Entrance. Some of the waters of the southern branch pass near the coast of southern Vancouver Island where they became the southerly flowing California Current. Along the whole coast the ocean currents follow a serpentine path to and from shore (Tully and Doe, 1953).

The coastal counter-current, carrying the fresh waters drained from the land, tends to flow northward along the coast from San Diego to the Aleutian Islands of Alaska. Off the west coast of Vancouver Island, this current flows northwestward regardless of the ebb and flow of the tidal currents, though part of it is dissipated in the gyros of the ocean current. The counter-currents are strongest in May and June, when the spring freshets of the big rivers reach the sea. At this time the counter-currents are ten or more miles wide with a layer of brackish water at the surface, but later in the season they recede as the river flow decreases (Tully, 1953). A marginal turbulence between the coastal and ocean currents is present, and zones of sinking and rising waters occur throughout the area (Tully, 1937).

It was expected that there would be a varied chaetognath fauna along the western Canadian coast, since 15 species have been identified from the Philip-

pines, 18 from Japan and 13 from San Diego. However, four species only, representing two genera, were collected from the areas sampled in Canada. One additional species (*Sagitta planctonis*) has been identified from the region by J. M. Thomson of Australia for R. J. Le Brasseur, student of the University of British Columbia. The specimen may have been an isolated, immigrant, since the species was not found in the present survey, either in the region from which it had been reported or from any other. Since no stations were located in the deep waters off the coast beyond the continental shelf, future work in the deep ocean could reveal the presence of many more species.

The species found at any time in the British Columbia waters and their presence or absence in the other three regions where the chaetognath fauna has been investigated in the north Pacific ocean are shown in Table I.

The distribution is of interest, though there is insufficient information about the life histories of the different species, their habitats and their occurrence in intervening areas to draw significant conclusions.

TABLE I. Occurrence of British Columbia chaetognaths in other areas of the North Pacific.

British Columbia (in descending order of abundance)	Philippines (Michael, 1919)	Japan (Tokioka, 1940)	California (Michael, 1911)
Sagitta elegans	−	+	−
Eukrohnia hamata	+	−	+
Sagitta lyra	−	+	+
Sagitta decipiens	+	+	−
Sagitta planctonis	+	−	+

ANATOMY OF CHAETOGNATHS

Arrow worms are slender, transparent animals, the largest of which may reach a length of over seven centimeters. The body is divided by transverse septa into head, trunk and tail regions. Delicate fins along the sides are used for balance and buoyancy rather than for swimming, and there is also a caudal fin at the end of the tail. On the head are two paired rows of very short teeth, besides longer lateral hooks, used for seizing prey and putting it into the ventral mouth. A hood, originating in the neck region, partly covers the hooks. The eyes usually appear as two dark spots on the dorsal surface of the head. On the trunk a prominent structure is the swollen ventral ganglion located on the ventral surface toward the anterior end. Just anterior to the tail septum is the anal opening, and the surrounding tissues may be quite enlarged and protruding. Spots consisting of groups of sensory fibers are scattered regularly over the surface of the body and the fins.

Since the animals are transparent, the internal organs are also visible. The intestine is a straight tube leading from the mouth to the anus, the part in the head often being called the pharynx. Mature or maturing specimens have ovaries extending forward from the tail septum and seminal vesicles projecting laterally at the sides of the tail. Chaetognaths usually have longitudinal muscles only, and they swim in short, vibrating spurts.

The most obvious external and internal structures, which include those necessary for species identification, are drawn and labeled in Figure 1.[4]

Very small chaetognaths just emerged from the egg look like adults, though the proportions are different. The tail is longer, and the ventral ganglion, which does not increase much in size as the animal grows in length, is almost as long as the trunk. Meek (1928) presents an excellent diagram of the relative rates of growth of the various parts of the body of *Sagitta elegans*. The animals lengthen considerably before they start to mature, though the length at maturity is greatly influenced by the temperature of the water. Individuals of a given species mature earlier in warmer water, and in cold water often grow to a comparatively large size before maturing.

Chaetognaths are hermaphroditic and protandrous. A description of the maturity stages of *Sagitta elegans*, as observed during this study, will serve to illustrate fairly well the development of chaetognaths in general. The male reproductive organs are located in the tail, and eventually the entire tail becomes completely filled with sperms. Even before the slightest trace of ovaries can be seen, the tail may be so full of spermatocytes and sperms as to be opaque and yellow in color. The seminal vesicles then begin to push out at the sides of the tail. At this time, short, rod-like ovaries make their appearance. The seminal vesicles grow rapidly and the sperms are extruded by the time the ovaries are completely mature. The tail is then left empty and transparent, and the spent seminal vesicles are ragged-looking. The shape of the seminal vesicles and their location on the tail in relation to the lateral and tail fins are of specific importance, and when present they are an excellent recognition characteristic.

As the ovaries mature they elongate, the length to which they reach anteriorly varying with age and species. In the early stages they appear slender and rod-like, but as some of the eggs increase in size, the ovaries become broader and bunchy in appearance. In mature individuals the ovaries have reached their extreme length and all the eggs are large. Animals that are about spent have a few large eggs scattered along the length of the ovaries with empty spaces between.

Extrusion of the eggs appears to complete the life cycle for almost all species of chaetognaths, though *Sagitta enflata*, according to Thomson (1947), is thought to have two cycles of reproduction. Of *Sagitta elegans* Meek (1928) says, "It is evident that, after spawning as females, *Sagitta* disappears, or apparently disappears, and it may be therefore that the end of maturity is also the end event of life". In discussing this aspect of the chaetognath life history, Meek stated that two generations of *S. elegans* seem to develop each year in the Northumbrian waters, one spawning in the spring and the other in the autumn. On the other hand, Russell (1933) says that "*Sagitta* is an animal which passes through several generations in the year, possibly five or six according to the species". In the cold

[4]The original drawings submitted by the author were lost in transit. Replacements were drawn in the Zoology Department of the University of British Columbia from photostats made earlier of the unpolished drawings. The author did not have the opportunity of checking the illustrations before publication, and a number of inaccuracies are apparent. For correct proportions and accurate detail, please refer to the photostats in the thesis.

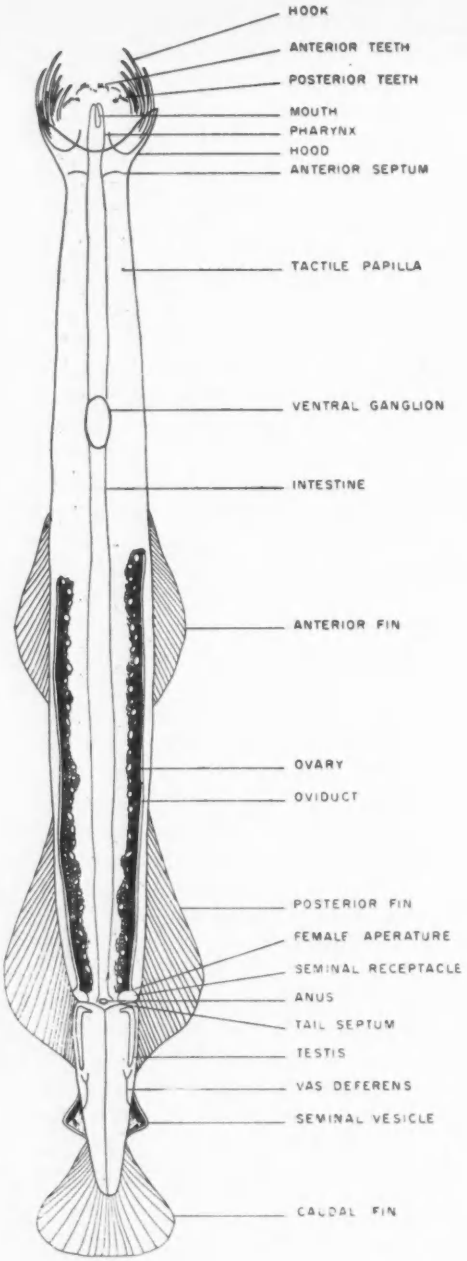

FIGURE 1. *Sagitta*, diagrammatic drawing, ventral view.

polar waters of the Canadian eastern Arctic with temperatures of 1°C. or below, Dunbar (1941) found that the arctic sub-species of *Sagitta elegans* takes two years to reach maturity.

MATERIAL

The collections studied in this investigation were made by Dr. Robert F. Scagel, assistant professor of oceanography, during cruises of the C.G.N.V. *Cancolim II* in 1953 and of the C.N.A.V. *Ehkoli* in 1954. Almost all of the material was collected from June 12 to September 5, 1953, but in one region hauls were made on May 21 and 22, 1954. The stations were located in a variety of areas extending from the northernmost to the southernmost part of the Pacific coast of Canada, as indicated in Figure 2, and a study of the hauls gives a fairly accurate overall picture of the distribution of the chaetognath population in British Columbia at that time. Since the cruises were not planned for the purpose of this investigation, and plankton hauls were not made at every station occupied, it is fortunate that the stations at which hauls were made were so well placed for a population and distribution study of the entire region. The material available

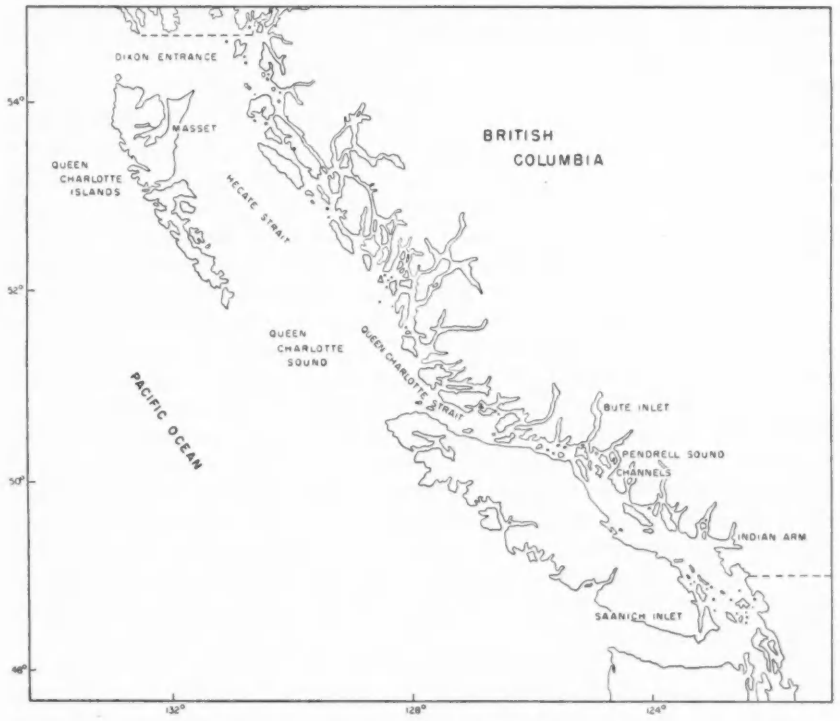

FIGURE 2. Coast of western Canada, and adjacent parts of the United States, showing regions investigated.

for study included 139 hauls from 113 stations. Several hauls were made at some of the stations where the ship was anchored for extensive oceanographic surveys.

The hauls were made with a No. 10 nylon net having a diameter of 30 inches, the net being drawn vertically from the bottom to the surface. At every station data were recorded for temperatures, salinities and oxygen content at various levels. Since these data are indispensable in a distribution study, as much use as possible was made of the information. However, when specimens are taken in vertical hauls, there is no way of knowing at what depth the chaetognaths were taken and what oceanographic conditions actually prevailed at that particular level.

The samples were preserved in 4% formalin, which has been found to be the best preservative for chaetognaths, and most of the specimens were in very good condition.

EXAMINATION AND RECORDING OF DATA

Chaetognaths do not require staining for examination. If the specimens have been well preserved, they can be examined most easily by floating them in a little of the 4% formalin in which they have been preserved.

After the species have become easily recognizable, the use of the binocular microscope is all that is usually required, but to differentiate some of the details necessary for the original identifications, especially the teeth, a compound microscope must be used, and hollow-cone illumination was found to be a distinct advantage. With this illumination a green light filter proved to be generally effective, though polarized light and a phase retardation plate were also useful. The special lighting technique used was developed by Dr. Kenneth Graham, professor of forest entomology of the University of British Columbia. The details in regard to increasing image contrast by the use of hollow-cone illumination are described by Mathews (1953).

To determine the number of specimens present in each sample, the entire sample was examined and all specimens were removed. These were counted and the numbers of mature, maturing and immature individuals were recorded. The sizes of the largest and smallest specimens of each were also recorded. Individuals of *Sagitta elegans* were classified as mature if they had well developed ovaries and seminal vesicles; maturing if they had rod-like ovaries and also had seminal vesicles; and immature if there were no seminal vesicles, even though in some cases very small ovaries could be seen. Individuals of the other three species were designated as maturing if they had ovaries, even though there were no seminal vesicles, and immature if they had no ovaries.

Complete data on file in the library of the University of British Columbia (Lea, 1954) give locations and depths of all stations; temperatures, salinities and circulation in the areas; and details as to numbers, sizes and maturity stages of the specimens obtained in all hauls.

SPECIES IN BRITISH COLUMBIA

Four species only, representing two genera, were found to occur in the area studied. These species are:

Sagitta elegans Verrill (1873)
Sagitta lyra Krohn (1853)
Sagitta decipiens Fowler (1905)
Eukrohnia hamata Möbius (1875)

Two of these species, *Sagitta elegans* and *Eukrohnia hamata*, were common, while the other two were found in small numbers only in the open ocean waters near the Queen Charlotte Islands. It is not difficult to differentiate the species, but *S. elegans* presents some problems, since it varies from region to region sufficiently in transparency and proportions and in numbers of hooks and teeth to justify the recognition of three sub-species.

Eukrohnia hamata (Fig. 3)

This species, not as abundant as *S. elegans*, but apt to be present in small numbers in most regions of British Columbia, cannot be confused with any other. Even in a dish full of chaetognaths, it appears different to the naked eye. Specimens bent almost at right angles in the region of the ventral ganglion frequently prove to be this species. The bending may possibly be due to localized muscular disintegration following the animal's entrance into water of low salinity, as the species is an oceanic form. Ritter-Zahony (1911a) remarked that some individuals of *E. hamata* he observed were uncommonly transparent and appeared to be undergoing a slow muscular atrophy. Besides the bending, there is often marked curvature of the entire body. Also, the animals are ragged-looking along the sides, with debris in the form of copepods, other animals or algae frequently entangled in the lateral or tail fins or in the hooks.

Under the binocular microscope, *E. hamata* is conspicuous because of the large oil droplets in the intestines. In addition the hooks are usually spread, and there is a distinct neck, making the head appear broad. The fins, wide, delicate and sparsely rayed, one pair to each side, extend from in front of the ventral ganglion to halfway down the tail. The tail has an angular appearance, while other species have smoothly tapering tails. If the animal appears to have no eyes, one can be almost sure that the specimen is *E. hamata*, since individuals living in cold water have no pigment in their eyes (Thomson, 1947), and none of those found in British Columbia waters had pigment. Examination under the compound microscope reveals conspicuously serrated hooks in young specimens. Also, while most chaetognaths, including all the others found in British Columbia have two paired rows of teeth, *Eukrohnia* has only one paired row.

Out of the 1,018 individuals of *E. hamata* taken in the entire survey, 1,002 were immature, 15 had rod-like or short ovaries and only one was fully mature. The completely matured specimen had a peculiar appearance, with the trunk almost entirely filled with large eggs, and the tail swollen to about twice the size

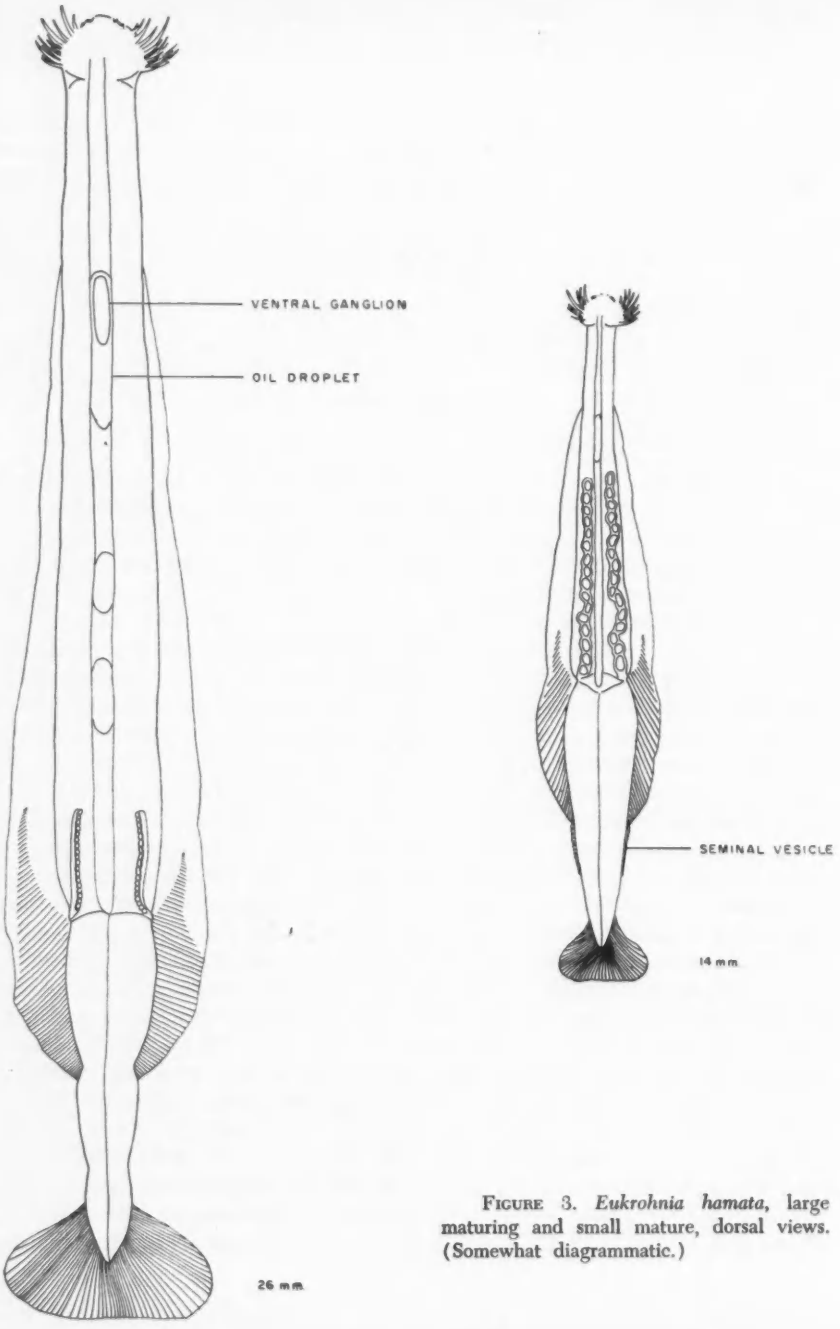

FIGURE 3. *Eukrohnia hamata*, large maturing and small mature, dorsal views. (Somewhat diagrammatic.)

of the trunk. Figure 3 shows a large maturing specimen with three conspicuous oil droplets and the much smaller mature individual mentioned above. Ritter-Zahony (1911c) states that *E. hamata* reaches a length of 43 millimeters, but the largest taken in British Columbia measured 27 millimeters.

Though *E. hamata* is an oceanic form, unlike the other deep sea species it had found its way into the shallow waters of many of the inland passages and inlets of British Columbia. According to Ritter-Zahony (1911b), this species occurs in the tropics at depths of from 400 to 1,000 meters, but in the north it may be found near the surface as well as in the deep waters. These surface individuals could easily be transported by currents into the shallow coastal waters.

Very little can be determined about temperatures and salinities favorable to animals collected in vertical hauls. However, not many *E. hamata* were found where the bottom temperatures were over 8.5°C., and temperatures above 10°C. in shallow areas appeared to be effective barriers to the species. Salinities below 27 to 28 ‰ along with higher temperatures over shallow sills seemed to prevent the entrance of *E. hamata* into two of the inlets.

Sagitta elegans (Fig. 4)

This is the most abundant and widely distributed species in the region. *S. elegans*, unlike *E. hamata*, has two pairs of fins along the sides. The posterior ones are relatively long, broad, firm and oval-shaped, with a greater proportion on the trunk than on the tail. The anterior fins are some distance back from the ventral ganglion and are shorter and narrower than the posterior ones. Both pairs are completely rayed. Sometimes on preservation the sides of the trunk fold in, and the anterior fins are folded out of sight. If the fins cannot be seen, they will be exposed by flattening the body gently in the fin region.

The neck of *S. elegans* is broad, and the head generally does not look any wider than the body. However, should the animal be killed in the act of eating, the head will appear very wide, and the hooks may even be inserted into the mouth. Very relaxed specimens may have the hooks spread.

S. elegans is usually quite stiff and sometimes opaque, but most specimens taken in British Columbia were transparent and many were flabby. The species usually has 10 hooks, but though the number varies from 8 to 13, there are not less than 8. The only other species in the region with which it could be confused, *S. decipiens*, has no more than 7 hooks. The teeth of *S. elegans* are difficult to see and count, especially in the more opaque specimens, but there are two paired rows of them, and they increase in number as the animals grow longer.

Mature individuals have prominent, conical seminal vesicles on each side of the tail, either touching the tail fin or very close to it, and distant from the posterior fins. The eggs are large and the ovaries extend well forward into the body cavity, often into the region of the anterior fins. The younger but maturing specimens have flatter seminal vesicles and slender rod-like ovaries, very short and inconspicuous in the youngest animals, but elongated and plainly visible in those approaching maturity.

The identification of *S. elegans* resulted in the disclosure of an error in

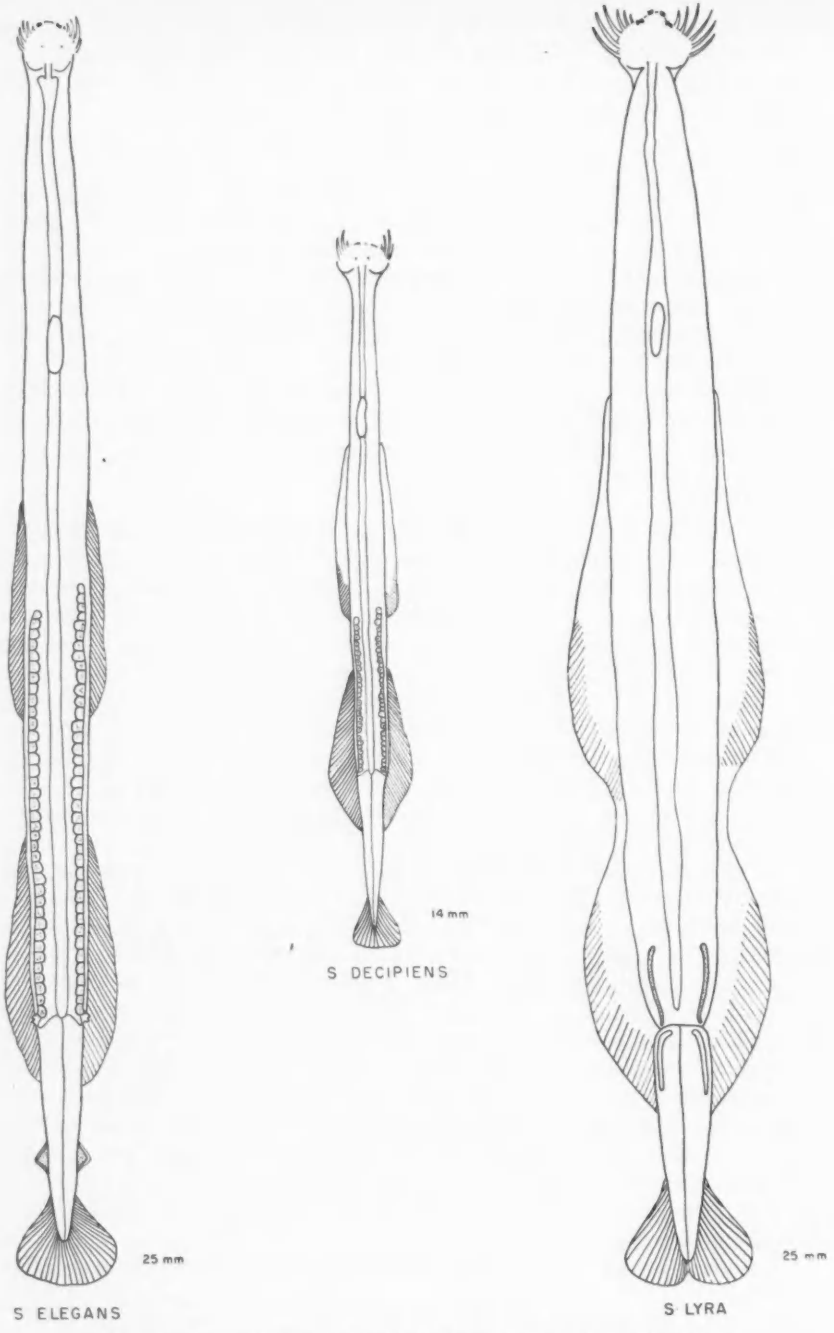

FIGURE 4. *Sagitta elegans*, *Sagitta decipiens*, and *Sagitta lyra*, dorsal views. (Somewhat diagrammatic.)

Michael's work (1911, 1919) in which he located the seminal vesicles adjacent to the posterior fins rather than adjacent to the tail fin.

The sub-species of S. *elegans*, as designated by Ritter-Zahony (1911c), are S. *elegans elegans*, S. *e. arctica*, and S. *e. baltica*. Both Ritter-Zahony and more recently Huntsman (1919), who investigated the sub-specific differences thoroughly for the species in eastern Canadian waters, agree as to the general characteristics separating them. Huntsman believes that the differences are caused by different temperatures during development, but Ritter-Zahony (1911b) attributes them to variations in the salinity of the water.

In the distributional survey of the species in western Canadian waters, no attempt was made to differentiate the sub-species. Neither did Huntsman find it worth while to consider them separately in his work in eastern Canada. Fraser (1937) also observed that there is very little clear-cut difference between the varieties of S. *elegans*, and that a complete sequence of types can be found.

In the entire survey, 9,564 specimens of S. *elegans* were taken. Of this number, 654 were mature, 473 maturing and 8,437 were immature. There were almost ten times as many S. *elegans* as there were *E. hamata*, which was second in abundance. In addition, 12% of the specimens of S. *elegans* were mature or maturing, compared with 2% for *E. hamata*. The largest British Columbia specimen of S. *elegans* was an immature one that measured 35 millimeters, but the longest recorded individual is a 52-millimeter specimen taken by Huntsman from water below the freezing point in the Bay of Islands.

Very few specimens were taken in British Columbia where the bottom temperatures were over 9°C., though immature specimens appeared to have been carried by currents into warmer regions in some areas. The summer surface temperatures varied between 7° and 19°C. As to salinities, specimens were not found at salinities below about 26.5‰ or much above 32 to 33‰. According to Redfield and Beale (1940), S. *elegans* is "an inhabitant of the upper levels", but we have no way of knowing at the present time at what depth the species lives in western Canada.

S. *elegans* has now been definitely established as the dominant species of chaetognath on both sides of the northern Atlantic and Pacific oceans, living in the cold, less saline waters of the continental shelves. In eastern Canada, Huntsman calls it "the characteristic *Sagitta* of our Atlantic waters", because of its general occurrence in the shallow water all along the coast. Very few specimens were collected by him in the deep waters beyond the continental shelf. Tokioka (1940) states that S. *elegans* is common in the cold waters of northeast Korea. Ritter-Zahony (1911b) found that it inhabited the northern European coasts, and Meek (1928) found that it was most often the dominant species in the Northumbrian plankton, while Fraser (1937) stated that it was dominant where Atlantic water mixes with the coastal waters of western and northern Scotland. The species does not occur in the southern hemisphere.

Sagitta lyra (Fig. 4)

This species is strikingly different from either *E. hamata* or S. *elegans*. The body is flabby and exceedingly transparent. The entire trunk appears wide, con-

stricting abruptly at the neck and also at the tail septum. The head is broad and, in contrast to the transparency of the body, is opaque, while the tail is noticeably slender and very transparent. The two pairs of lateral fins are delicate and sparsely rayed, the anterior ones being longer than the posterior. Because the fins are joined together, they appear almost like the single lateral fins of *E. hamata;* however they do not extend as far forward, reaching just short of the ventral ganglion rather than extending anterior to it. The caudal fins appear both delicate and unusually large. The rich-brown-colored hooks are conspicuous in comparison with the tan ones of the other species. The location of the anal opening is distinctive in *S. lyra.* In most species, including the others found in British Columbia, the opening is adjacent to the tail septum, but in *S. lyra* it is very definitely anterior to the tail septum. The teeth of *S. lyra* are also characteristic. They are often very few in number, and the anterior ones are long and project upward. The western Canadian specimens had only 2 to 4 anterior teeth and 2 to 7 posterior ones in each row, but the number is variable, and large specimens may have as many as 8 anterior teeth on each side and up to 12 in the posterior rows.

Of the 6 specimens taken, only 2 were maturing and had very slender rod-like ovaries. The longest one, 28 millimeters, had seminal vesicles just starting to develop. Mature specimens have small, conical ones lying halfway between the posterior and tail fins (Ritter-Zahony, 1911a). In the transparent tail, the male reproductive organs are plainly visible. This species grows to a comparatively large size, and while animals over 40 to 50 millimeters are seldom captured, Ritter-Zahony (1911a) gives 71 millimeters as the maximum size of *S. gazellae,* which is now considered the cold water form of *S. lyra.*

S. lyra is an almost cosmopolitan oceanic form usually found at a depth of 300 to 1,000 meters, according to Ritter-Zahony (1911b). He found the young ones in the epiplankton and the mature ones deeper in the mesoplankton. The specimens obtained in the British Columbia region were taken along the west coast of the Queen Charlotte Islands, none occurring in any of the inland waters.

Sagitta decipiens (Fig. 4)

This species resembles *S. elegans* somewhat. The body is stiff and transparent and the fins delicate. The lateral fins are separated as in *S. elegans,* but the anterior ones are longer than the posterior and reach almost to the ventral ganglion. The caudal fin is small, and the tail is proportionately longer than it is in the other two species of *Sagitta* in the region. In those taken the tail was 25% of the total body length, but the possible range generally given is 20 to 31%. Fowler (1905), in his original description, gives 25 to 40%. Compared with the usual 16 to 20% for *S. elegans* and 16% for *S. lyra,* 25% is noticeable. The head is usually definitely wider than the body, rather rectangular in shape, and also quite transparent. The hooks are slender, scarcely pigmented and few in number, varying from 5 to 7. Specimens with 5, 6 and 7 were observed. *S. elegans* does not have less than 8. The eyes of *S. decipiens* are characteristic and different from those of other chaetognaths (Ritter-Zahony, 1911a). They are longer than wide,

and the pigmented parts of each look like two joined slender beads. The species is a small one, seldom reaching 15 millimeters. Though Ritter-Zahony (1911c) stated that it attained a size of 20 millimeters, Thomson (1947) gives 12 to 13 millimeters for mature specimens in Australia. The largest taken in British Columbia was 14 millimeters long and not fully mature.

Four excellent specimens of S. *decipiens* were taken, as well as three others damaged beyond certain identification. The four that were definitely S. *decipiens* had well developed ovaries, the longest reaching to the posterior end of the anterior fins, but none had seminal vesicles. The tails were clear, and though one contained quite a number of transparent sperms, the tail was not opaque as in S. *elegans* at the same stage of maturity. Neither were the tails as transparent as those of S. *lyra,* since the internal male reproductive organs were not visible. Ritter-Zahony (1911a) and Michael (1919) have pictured the seminal vesicles of S. *decipieus* as comma-shaped, widest at the anterior end, and adjacent to the tail fin.

S. *decipiens,* like *E. hamata* and S. *lyra,* is an oceanic form, and according to Ritter-Zahony (1911b) is found between 200 and 1,200 meters. As with S. *lyra,* the mature forms are also found at the greater depths. The British Columbia specimens were taken in two hauls of 249 and 366 meters in open ocean areas.

Corroborative identifications of S. *elegans,* S. *lyra* and S. *decipiens* were made by Dr. J. M. Thomson, senior research officer, Marine Biological Laboratory, Cronulla, Australia.

It is not suggested that all species of chaetognaths which occur in British Columbia waters have been obtained. In the present investigation, S. *decipiens* is reported for the first time, and S. *planctonis* was not taken. Other species undoubtedly occur in the deep oceanic waters and could be collected in offshore hauls. Also, some of these might be carried into coastal waters from time to time.

KEYS TO THE SPECIES OF BRITISH COLUMBIA CHAETOGNATHS

The following keys were constructed for the identification of specimens collected during this investigation. It is intended that the use of the keys, with the aid of the descriptions and drawings, will enable one to identify the species most commonly found in the area. Because so few species are involved, difficult structural characteristics, such as the numbers of teeth and structure and articulation of parts of the hooks, can be avoided in the keys. The first key is for use with well-preserved individuals with all fins present, the characteristics being obvious enough for identification under a binocular microscope only. In the other key, no use of the fins is made, but examination with a compound microscope, and perhaps some manipulation, is necessary for counting the hooks.

Key for Well-Preserved Specimens

1. One pair of lateral fins or two connected pairs 2
   2. No pigment in the eyes; anal opening at tail septum; oil droplets in the intestine ..... *E. hamata*

2. Eyes pigmented; anal opening anterior to tail septum; no oil droplets in the intestine ..... *S. lyra*

1. Two pairs of lateral fins widely separated 3

3. Anterior fins longer than posterior and reaching almost to ventral ganglion; hooks 5–7, usually 6 ..... *S. decipiens*

3. Anterior fins shorter than posterior and some distance behind ventral ganglion; hooks 8–13, usually 10 ..... *S. elegans*

KEY FOR SPECIMENS WITH DAMAGED FINS

1. Anal opening anterior to tail septum ..... *S. lyra*

1. Anal opening at tail septum 2

2. No pigment in eyes ..... *E. hamata*

2. Eyes pigmented 3

3. Hooks 5–7 ..... *S. decipiens*

3. Hooks 8–13 ..... *S. elegans*

DISTRIBUTION AND FREQUENCY OF OCCURRENCE

The stations studied in the British Columbia survey were located in 11 representative areas, as indicated on the map (Fig. 2), extending along the entire coast of Canada, from Saanich Inlet in the south to Dixon Entrance in the north. The coastline is rugged and cut by many deep fjords. Numerous rivers of glacial origin discharge large enough volumes of fresh water into the sea to have a marked effect upon the fauna and flora of the region. The distribution of the chaetognaths reflects both the geographic and oceanographic character of the area (Table II).

The areas covered in the survey are listed in order from south to north, and the number of stations occupied and number of hauls made are indicated, besides the total numbers of each species of chaetognath taken in the regions.

It is obvious that *S. elegans*, the characteristic species of mixed coastal waters, occurred in abundance in most areas, and was present at least in small numbers in every region sampled.

The oceanic *E. hamata* was most abundant in localities connected with the open ocean, though a few individuals were found in most of the inland passages and inlets. No specimens were taken in the three inlets, Indian Arm, Pendrell Sound and Masset Sound and Inlet. The mouths of Indian Arm and Masset Sound were blocked by shallow, warm water in the summer, and the warm temperature and lack of circulation in Pendrell Sound are a barrier to other plankton animals as well as to chaetognaths. As mentioned previously, few specimens of *E. hamata* were maturing. Also, no very young ones were taken from the inland waters, and it appears that, on the whole in most localities, those present must have been migrants carried there by the currents. Redfield and Beale (1940) found the same situation in the Gulf of Maine, where *E. hamata* also ranked second in abundance to *S. elegans*. They concluded that because *E. hamata* lives near the surface of the ocean, it comes into the Gulf with the

TABLE II. Distribution of chaetognaths by areas.

Area	No. sta.	No. hauls	*S. elegans*	*E. hamata*	*S. lyra*	*S. decipiens*
Saanich Inlet	19	19	1,456	23		
Indian Arm	7(4)	12	837			
Pendrell Sound	3	3	55			
Chan. North End Str. of Georgia	3	3	204	1		
Bute Inlet	8	26	594	17		
Queen Charlotte Strait	19	19	498	8		
Queen Charlotte Sound	2	2	342	58		3
Hecate Strait	9	10	9	1		
Dixon Entrance	19	19	2,656	836		1+3? 4
Masset Sound and Inlet	4	4	1,847			
West Coast Queen Charl. Is.	20	22	1,066	74	6	
TOTALS	113	139	9,564	1,018	6	4+3?

currents, where, as a terminal migrant from other regions in which it breeds endemically, it lives as long as circumstances permit and dies without leaving progeny.

S. lyra, a widely distributed species of the deep sea, is rarely taken near shore. The six specimens obtained were all found off the west coast of the Queen Charlotte Islands very near the edge of the continental shelf. Wailes (1929) records *lyra* as "*myra*" from the west coast of Vancouver Island and also from the Strait of Georgia, but gives neither exact locations nor times of year. In eastern Canada, Huntsman found its inner limit was 60 miles off the continental shelf in May and June, but that it was near the edge of the shelf in July and August. The British Columbia specimens in the present survey were taken in August within a mile or two of the continental shelf.

A less common oceanic form is *S. decipiens*. The two regions where it was taken are open coast areas, one in Queen Charlotte Sound and the other at the outer end of Dixon Entrance. At least four specimens were taken in addition to the three damaged portions of chaetognaths which appeared to be *S. decipiens* also. *E. hamata* was unusually abundant at the stations where *S. decipiens* was found, and it appears that the inner limits of *S. decipiens* overlap somewhat with the outer limits of *S. elegans* and the region of increasing abundance of *E. hamata*.

DISTRIBUTION IN EACH AREA

The 11 areas sampled are discussed separately, starting with the southernmost and working northward to the region most approaching oceanic conditions off the west coast of the Queen Charlotte Islands. Evident peculiarities in the

distribution of the animals are pointed out, and oceanographic factors possibly influencing the distribution are suggested. Each area is quite different in geography and water conditions, a fact which adds to the value of the survey.

Saanich Inlet

The material from Saanish Inlet was collected on May 21 and 22, 1954. Twenty stations were occupied, and most of the samples taken were examined.

S. elegans was found to be abundant in the region, and all maturity stages were present, indicating that water conditions must be favorable and that the species is probably endemic.

E. hamata was also present in the Inlet, though in small numbers. Only 23 specimens, all immature and relatively large, were taken in the deeper hauls. One could assume, since there were so few individuals, that the animals had been carried into the region by currents and were not indigenous to the area.

Indian Arm

The samples from Indian Arm were collected on September 4 and 5, 1953. Twelve hauls represent seven stations in four areas.

S. elegans constitutes the entire chaetognath population of Indian Arm, this inlet being one of three among all the areas sampled where no *E. hamata* were taken. No chaetognaths were found in the relatively warm, brackish waters at the head of the Arm, but halfway down the inlet in deeper, colder and more saline waters, *S. elegans* was abundant and in all maturity stages. Very few specimens were taken near the mouth, where shallow, warm, less saline water appears to be a barrier to the chaetognaths in the Arm as well as to prevent the entrance of migrants from the outside, such as the oceanic *E. hamata*.

Pendrell Sound

Three hauls made in Pendrell Sound on August 24 and 25, 1953, were examined. The Sound was one of the three regions were *S. elegans* was the only chaetognath present. However, the distribution of this species was unique in that the population was all concentrated toward the entrance, and all specimens taken were small and immature. Since there is very little circulation in the Sound, the animals must have entered at the mouth through random swimming. Lack of food supply towards the head may have been a factor in preventing deeper penetration into the inlet. Examination of the specimens during this survey showed copepods to be an important source of food for chaetognaths, and in Pendrell Sound the copepods also are concentrated towards the entrance (Le Brasseur, 1954).

Channels at the North End of the Strait of Georgia

Three hauls were made on August 23, 1953 in the channels at the north end of the Strait of Georgia. At the southern stations toward Pendrell Sound, *S. elegans* only was found, and though it was present in some numbers, all individuals were immature. Farther north, towards the mouth of Bute Inlet,

all maturity stages of this species occurred and, in addition, one rather large, immature *E. hamata* was taken. Since both species occur in Bute Inlet in all maturity stages, and the water conditions in the channel are similar to those in Bute, one could expect to find a similar population just outside the mouth of the Inlet.

Bute Inlet

Twenty-six hauls were made at eight stations in Bute Inlet from August 20 to 23, 1953. These stations were approximately equidistant along the entire length of the Inlet. Both *S. elegans* and *E. hamata* occurred in all maturity stages. *S. elegans* was abundant only toward the mouth, though almost all of the specimens taken there were rather small and immature. In the center of the Inlet the population was not large, but a few individuals were mature or maturing. Toward the head, though even fewer specimens were taken, 30% of them were maturing.

E. hamata was not present in great numbers, but conditions in the Inlet appear to be favorable, to the extent that half of the few individuals taken were maturing. Also, the only fully mature specimen obtained throughout the entire survey (Fig. 3) came from the middle of Bute Inlet. All of the specimens of *E. hamata* taken were in the lower half of the Inlet, and most of these were towards the mouth.

Had the object been only to discover the distribution of *S. elegans* and *E. hamata* in the Inlet, it would not have been necessary to examine all the samples collected at three of the stations where hauls were made at regular intervals over a period of 24 hours. However, *S. planctonis* had been reported from the area on the basis of a specimen taken by R. Le Brasseur and identified by J. M. Thomson. Ordinarily one would not expect this deep sea species to survive a journey into the less saline inland waters, and none was taken in the 26 hauls available for this study.

Queen Charlotte Strait

There were 19 hauls made at 19 stations in Queen Charlotte Strait between June 12 and 16, 1953. *S. elegans* occurred in every haul, and there was at least one immature *E. hamata* in most hauls made in the channel, though there were none near the coastlines.

At the ocean end of the Strait, the specimens of *S. elegans* taken were small and immature. A greater number were taken in the central part of the Strait and quite a few of these were mature. The mature ones were both at mid-channel and along the north shore. Along the south shore the specimens were immature. It would appear that the animals were maturing in the mixed waters of the ebb tidal current which flows out along the northern side, while the immature forms are more widely distributed.

Since the eight specimens of *E. hamata* taken were small, immature and scattered near mid-channel, it seems likely that they were migrants brought in by the flood tide.

Queen Charlotte Sound

Only two hauls made in Queen Charlotte Sound on August 10, 1953, were available for examination. In one shallow haul of 42 meters just outside the entrance of Queen Charlotte Strait, a swarm of very small immature *S. elegans* was found. Few animals as small were taken in the Strait. Another swarm of these very small individuals was encountered at the other station farther off shore, and in addition, with them were great numbers of equally small *E. hamata*. In the inland waters only larger specimens of *E. hamata* had been taken, and the population had been scattered and sparse.

Of additional interest was the discovery in the offshore haul of three very fine, 12-millimeter specimens of *S. decipiens* with well-developed ovaries, but no seminal vesicles. The haul at 249 meters was not an especially deep one, and it would hardly be expected that a deep ocean species at an advanced stage of development would be found in that location, since Ritter-Zahony (1911b) gave the range of *S. decipiens* as 200 to 1,200 meters, the young inhabiting the epiplankton and the mature ones the mesoplankton. With the young of the coastal *S. elegans* and the oceanic *E. hamata* both in abundance, plus the deep sea *S. decipiens*, the station appears to be approaching the borderline between the oceanic and coastal fauna.

Hecate Strait

Ten hauls were made at nine stations at various parts of Hecate Strait from July 16 to 30, 1953, but in only two hauls were chaetognaths present, as much of the Strait is shallow and relatively warm. At two stations on the east side near the northern entrance, ten specimens, all immature, were taken. Nine of these were *S. elegans* and one was *E. hamata*. At the two stations the bottom temperatures of 8.4° and 9.5°C. were lower than at most of the other stations. *E. hamata* was in the haul where the bottom was both deepest and coldest.

Dixon Entrance

Nineteen hauls were made at 19 stations in Dixon Entrance between July 19 and 29, 1953. Five stations were about equidistant along the southern edge of the channel, and others were in various locations between the channel and the shores of Graham Island of the Queen Charlottes. The two westernmost of the channel hauls were deep ones made in the channel itself, and the other three were not far from the edge of it. Both *S. elegans* and *E. hamata* were found in large numbers in these channel hauls. At the seaward end of the Entrance, both species were very abundant, and there were quite a number of mature individuals. However, with progression eastward toward the mainland, both the population density and the number of mature animals decreases.

Considering the two western channel hauls, at the station well into the Entrance more specimens of *S. elegans* were taken than in any other locality in British Columbia. *E. hamata* was also present in unusually large numbers. At the station at the mouth of the Entrance the number of *S. elegans* diminished, and there was an even greater number of *E. hamata*. In fact there were more

E. hamata than S. *elegans*, reversing the proportion of the two species found in most hauls. Also, some of the specimens of *E. hamata* were maturing. Another unusual thing about this haul was the presence of an excellent 14-millimeter specimen of the deep sea S. *decipiens*, besides three doubtful portions of this species. The undamaged specimen had well-developed ovaries, but no seminal vesicles.

The continental shelf is very close to the west coast of the Queen Charlotte Islands, and the evidence of these hauls in Dixon Entrance points to the conclusion that the region of the continental shelf may form the outer limit for S. *elegans* and mark the inner boundary of the region most favorable to the oceanic forms. In a haul made in the open waters just outside Dixon Entrance, *E. hamata* only was found. This station could be beyond the limits of S. *elegans*.

The other hauls in Dixon Entrance were of interest, also, in the study of the distribution of the chaetognaths in the strait. The number of specimens decreased with the distance from the channel and approach toward the shore, and those that occurred were all immature. Along the coast no chaetognaths were taken in the nine hauls made. These hauls were in shallow water, but in other parts of British Columbia equally shallow hauls disclosed large populations of chaetognaths. An examination of the data for the temperatures of all the stations in Dixon Entrance leads to the conclusion that in these waters chaetognaths do not usually occur where temperatures are relatively high. None occurred where the bottom temperature was much over 9°C. They were most abundant where the bottom temperature was 5.5°C., and as the temperature increased, the numbers of chaetognaths decreased. In Hecate Strait, where many hauls were made without finding chaetognaths, the bottom temperatures were also high.

Masset Sound and Inlet

The material from four stations collected between July 20 and 25, 1953, was available for examination. One station was in Masset Sound, and three were in widely separated regions in Masset Inlet.

No chaetognaths were taken near the entrance of Masset Sound not far from Dixon Entrance, where the only haul in the Sound was made at a depth of 15 meters. This does not mean that none was present anywhere in the Sound, but since chaetognaths were also absent along the coastal waters of Dixon Entrance, it may be that in July there were no chaetognaths in the shallow, warm parts of the Sound.

In Masset Inlet S. *elegans* only was present, but it occurred in great abundance and in all sizes and maturity stages. Off the shoals at the eastern side, a swarm of extremely small individuals was encountered. In the one haul there were 1,201 specimens, mostly much under five millimeters in length. On the northern side of the Inlet, slightly larger specimens were fairly abundant, while at the western station, near the deepest part of the Inlet, there were hundreds of very large, opaque individuals. Fifty-seven per cent of these animals measured over 20 millimeters, and more were close to 30 millimeters than to 20. Fifty-five of the 490 specimens taken in the one haul were mature and four others were

maturing. For average size these were the largest specimens of S. *elegans* taken in this investigation, though there were a few almost as large in Saanich Inlet, and one extra large individual in Dixon Entrance measured 35 millimeters. Nine hauls were made at this same Masset station at three-hour intervals over a period of 24 hours. In only one were the specimens counted, but the other samples were inspected and found to contain approximately the same number of very large, opaque specimens as the sample counted, indicating that the large S. *elegans* were residents in the area and not a passing swarm.

The abundance of S. *elegans* in Masset Sound poses several problems. The temperatures where the immature specimens were found are higher than those found to be favorable in most of the British Columbia waters. Perhaps the very young of the species are not repelled by relatively high temperatures, since they were present in unusually large numbers where the temperature ranged from 14.6°C. at the surface to 12.3°C. at the bottom. In Queen Charlotte Sound where there were also swarms of immature S. *elegans* the temperature was colder, ranging between 11° and 8°C. from top to bottom. The high oxygen content of the water in Masset may offset seemingly unfavorable high temperatures. However, Davis (1950) found immature specimens of *Sagitta* were sometimes obtained in Florida waters in places where one would never find adults. He thought it was probable that the eggs had been carried by currents to less favorable regions, where the young are either killed in time or are retarded in their development.

West Coast of the Queen Charlotte Islands

The 22 hauls made along the west coast of the Queen Charlotte Islands between August 5 and 9, 1953, were located mostly in the numerous bays and inlets of that deeply serrated coastline. Though the edge of the continental shelf is only one to two miles off the west coast of the group, no hauls were made in the deep waters beyond the shelf.

In most of the bays and inlets there were no chaetognaths, but Van and Tasu Inlets were exceptions. In the one sample taken from Van Inlet, located at the southwest tip of the largest island, S. *elegans* was not only exceptionally abundant, though all specimens were unusually small, but the proportion of mature and maturing individuals to immatures was much higher than in any haul made in the other areas studied. Of the 805 animals obtained, 15% were mature, 19% maturing and 66% were immature. At this station there was a wide range of temperature from a high of 15°C. at the surface to 7°C. at the bottom. The water was somewhat less saline than the surface waters of the open Pacific. (Sverdrup, *et al.*, 1952, give 33.64‰ for the Pacific Ocean at 40°N.)

Similar oceanographic conditions prevailed in Tasu Inlet farther south, where five stations were occupied. S. *elegans* was again abundant, though fewer specimens were taken in each haul and none was mature. One small immature *E. hamata* was also found in the Inlet.

Two offshore hauls of unusual interest were made—one off Skidegate Narrows, which is between the two largest islands, the other off Cape St. James at the southern tip of the archipelago. At both of these stations, and also at a station

in Houston Stewart Channel toward the south, the oceanic S. *lyra* was found. The specimens at two of the stations were rather small and immature, but the three taken off Cape St. James were larger and two were maturing. These had rod-like ovaries and some spermatocytes could be seen in the tails. Since this species is a deep sea form, it was not surprising to find it near the continental shelf. Huntsman found S. *lyra* in association with S. *elegans* in one haul only in eastern Canadian waters, but in all three hauls in which S. *lyra* was taken in the west, S. *elegans* was also present, as was *E. hamata* in the two offshore hauls.

At the station off Cape St. James, where the maturing S. *lyra* were obtained, *E. hamata* surpassed S. *elegans* in numbers, as it did also at the outer channel station in Dixon Entrance. This fact, along with the absence of S. *elegans* from so many of the coastal hauls on the west side of the Queen Charlotte Islands, and the presence of S. *decipiens* in two equally exposed regions, seems to be conclusive evidence that the region of the continental shelf is the outer limit for S. *elegans* in western Canada, as it is elsewhere, and the inner boundary for exclusively oceanic forms. It is also the beginning of the region most favorable to *E. hamata*, which was found only in small numbers in the inland areas.

EVALUATION OF THE DATA

The present investigation serves as a basic over-all survey of the species of chaetognaths found in the area and of their general distribution. The missing parts of the picture suggest many interesting problems for future research. Questions about the life histories, breeding seasons and abundance at different seasons or from year to year arise, as well as those concerning the depths at which the different species live and the water conditions at those depths. One also is curious as to what facts would appear if some of the other areas were sampled, including waters beyond the continental shelf.

Considering the subject of chaetognaths as indicators of currents, all that can be said at this time is that a relative abundance of S. *elegans* along with a few *E. hamata* indicates mixed coastal waters. *E. hamata* in abundance together with S. *elegans* in diminishing numbers suggests the approach of the outer limits of the mixed waters. Should S. *lyra* or S. *decipiens* be obtained, the presence of oceanic water is indicated.

SUMMARY

1. A study of the chaetognaths of the coastal waters of western Canada was made to discover what species were present and to determine their distribution. Samples collected during the summers of 1953 and 1954 by the Institute of Oceanography of the University of British Columbia were available from 11 representative regions along the entire coastline. Four species, representing two genera, were found to occur. These species are: *Sagitta elegans*, *Sagitta lyra*, *Sagitta decipiens*, and *Eukrohnia hamata*.

2. *Sagitta elegans* proved to be the most abundant and widely distributed species, occurring at least in small numbers in every area sampled. Its presence indicated mixed coastal waters, its numbers diminishing toward the edge of the

3. *Eukrohnia hamata*, an oceanic form, also occurring near the surface in northern regions, had penetrated most areas in small numbers, principally as a migrant carried by the currents. Warm, shallow water of low salinity prevented its entrance into two inlets, and it was missing from another where there was little circulation. *E. hamata* was found in abundance toward the edge of the continental shelf and in regions where oceanic influence was predominant.

4. *Sagitta lyra*, a species of the deep sea, was taken in very small numbers from the waters approaching the edge of the continental shelf off the west coast of the Queen Charlotte Islands. It was restricted to oceanic waters, and did not occur in any of the inland channels and inlets.

5. *Sagitta decipiens*, a deep ocean form, was taken in two regions where oceanic conditions prevailed. A few specimens were obtained in Queen Charlotte Sound and at the ocean end of Dixon Entrance. Both *S. elegans* and *E. hamata* were present in large numbers in the hauls, but the stations were not far from the outer limits of *S. elegans*, and *E. hamata* was replacing *S. elegans* as the dominant species.

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The Trout Population of a Nova Scotia Lake as Affected by Habitable Water, Poisoning of the Shallows and Stocking[1,2]

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ABSTRACT

A stocking, partial-poisoning and creel census experiment was carried out on a stratified lake in an effort to increase the crop of speckled trout, *Salvelinus fontinalis*. Except for a single year in which adult trout were planted, a negligible proportion of the introduced trout was recaptured. Application annually for five years of about one-half part per million of derris dust to the three-meter zone of the lake during summer stratification produced a heavy kill of coarse fish without harming the trout. Shiner, *Notemigonus crysoleucas*, perch, *Perca flavescens* and chub, *Semotilus atromaculatus* were eliminated from the lake. Sucker, *Catostomus commersoni*, was drastically reduced. Killifish, *Fundulus diaphanus*, and eel, *Anguilla bostoniensis*, were not appreciably reduced, despite large annual kills. Smelt, *Osmerus mordax*, stickleback, *Gasterosteus aculeatus*, and trout, *Salvelinus fontinalis*, were killed in very small numbers during one or more poisoning years.

Three independent estimates of the effect of the experiment upon the trout production of the lake are put forward: (*a*) The decrease in mass of the fish competing with trout for food, when calculated from the annual kills, amounts to 40 kg. The pre-poisoning mass of trout was 85 kg., calculated from a capture-recapture census. Thus if trout replaced its competitors quantitatively, the standing crop of trout would be increased to 150%. (*b*) The volume-time of water (i.e. percentage of the lake volume multiplied by the fraction of a year) which would be made available to trout by removing competitors from the part of the lake where summer temperature conditions would limit trout to between 50 and 100% of their full activity is calculated. If trout occupied this volume-time at the same density as they did the more favourable water, the standing crop of trout would be increased to 240%. (*c*) The total yield of the lake to anglers showed a steady increase following poisoning, to about 230% of the control value, or from less than one pound per acre to nearly two pounds per acre. These three estimates agree very well, considering the errors inherent in the method.

INTRODUCTION

There have been many attempts to alter the population balance of lakes by poison. Most of this work has been directed towards the control of non-game fish in lakes where selective removal by angling has resulted in a dominance of those that were considered undesirable. Claims for success are many, but quantitative statements about the change in population which has followed poisoning are few. For such information it is necessary to have a census of some sort before the experiment starts and to measure the population changes for

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several years following poisoning. An attempt in this direction is made in the present paper.

The poison used was derris root. The history of this substance in agriculture and fisheries is outlined by Leonard (1938) who reports on its relevant properties. In earlier experiments attempts were made to kill all the fish in lakes, but later there have also been reports on partial poisoning (Greenbank, 1940). Partial poisoning is most suitably carried out in stratified lakes, since it has been observed that the poison does not penetrate the depths (Clemens and Martin, 1952). In Greenbank's experiments the trout and suckers, mainly in the deeper waters of the lake, were relatively unharmed, while the kill of warm-water fish, perch, rock bass and largemouth black bass was practically complete. Greenbank concluded that in lakes deep enough for species segregation selective poisoning could be carried on satisfactorily.

Derris root is a fairly specific fish poison. It has little effect upon aquatic invertebrates except possibly planktonic crustaceans (Smith, 1939; Hooper, 1948). Leeches and dragonflies may be affected by the poisoning (Brown and Ball, 1942).

The toxicity of rotenone does not last very long. One or two days may remove its poisoning effect (Leonard, 1938), or the toxicity may last several days (Clemens and Martin, 1952). Toxicity is markedly affected by temperature. Thus according to Leonard (1938), Q_{10} for killing would be somewhat more than 2, in the range of summer pond temperatures. The disappearance of water toxicity is also slowed up by low temperatures, so that lakes poisoned late in autumn may remain toxic to fish until the seasonal turnover of water in the spring (Siegler and Pillsbury, 1946).

THE LAKE

Copper Lake is on the border between Antigonish County and Guysborough County, Nova Scotia, three miles east of Lochaber. The regional bedrock is composed of mixed metamorphic and sedimentary rocks of middle Devonian age. The lake was selected because it had previously been subjected to a stocking program combined with creel census (Smith, 1948).

Set in cultivated hills, the lake shore is gravel with some sand and mud and occasional rubble. Vegetation is in general scarce, a list being given in Table I. There are some patches of *Nitella* and *Chara, Nymphaea, Sparganium fluctuans, Eleocharis Robbinsii* and *Potamogeton gramineus f. maximus. Isoetes, Lobelia* and *Eriocaulon* occur, but are nowhere abundant.

Plankton tows taken on two occasions gave similar results. The most abundant organism was *Diaptomus minutus* with *Holopedium gibberum, Bosmina, Difflugia* and *Anabena* occasionally abundant. The net plankton was about 15 mgm. dry weight per cubic metre. The fish population of the lake is discussed below.

The dimensions and physical characteristics of Copper Lake are shown in Figure 1. The poisoning of the shallow zone was carried out to the three-metre line, shown as a shaded area in Figure 1. The area of the lake is 21.6 hectares, its maximum depth about 15 metres and the volume is approximately 1.2×10^6

TABLE I. List of plants in Copper Lake. A—locally abundant; C—common; S—scarce; R—rare.

SUBMERGED AND FLOATING SPECIES

Nitella, A
Chara, A
Isoetes Braunii Dur., C
Sparganium fluctuans (Morong) Robinson, S
Potamogeton amplifolius Tuckerm., R
P. gramineus f. *maximus* Morong ex Bennett, C
P. epihydrus v. *Nuttallii* (C. & S.) Fern., S
P. pusillus L., R
P. Spirillus Tuckerm., S
Najas flexilis (Willd.) Rostk. & Schmidt, S
Nymphaea odorata Ait., S
Hypericum ellipticum f. *aquaticum* Fassett, R

EMERGENT SPECIES

Glyceria borealis (Nash) Batchelder, R
Eleocharis Robbinsii Oakes, A
Eriocaulon septangulare With., C
Pontederia cordata L., S
Juncus militaris Bigel., R
J. militaris f. *subnudus* Fern., R
Myriophyllum tenellum Bigel., R
Sium suave Walt., S
Lobelia Dortmanna L., C

SHORELINE VEGETATION

Sparganium androcladum (Englem.) Morong, R
Glyceria canadensis (Michx.) Trin., R
G. striata (Lam.) Hitchc., R
Eleocharis obtusa (Willd.) Schultes, R
Scirpus rubrotinctus Fern., A
S. atrocinctus Fern., R
Carex stipata Muhl., R
Juncus bufonius L., R
J. articulatus L., R
Polygonum sagittatum L., R
Hypericum ellipticum Hook., R
Lysimachia terrestris (L.) BSP., A
Myosotis laxa Lehm., R
Scutellaria epilobiifolia Hamilton, R
Mentha arvensis L., R
Chelone glabra v. *ochroleuca* Pennell & Wherry, R
Eupatorium maculatum L., R

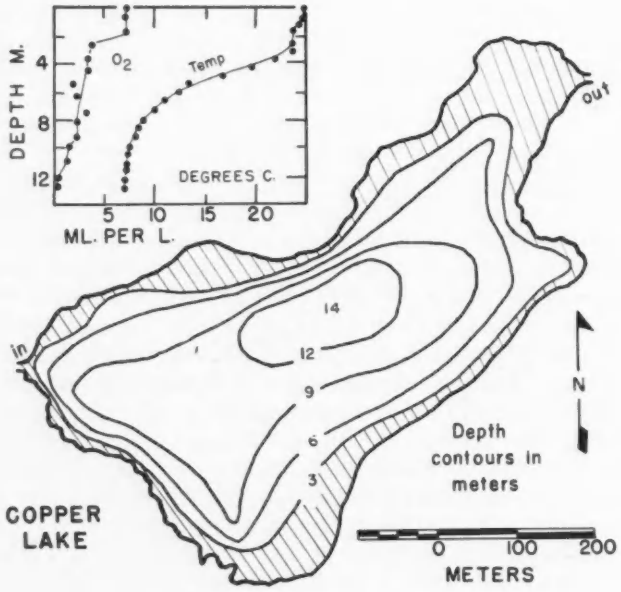

FIGURE 1. Contour map of the lake used for experiments. The small inserted graph, showing midsummer values of oxygen and temperature, indicates that the lake is stratified and that oxygen is used up in the hypolimnion.

cubic metres. The small diagram included in Figure 1 shows that in summer the lake is clearly stratified and exhibits a decline in oxygen below the thermocline.

In the spring of 1947 a rough census was attempted of the number of trout in Copper Lake. The technique, which is in common use, consists of taking as many fish as possible by angling, marking them, and returning them to the water. After a rest period the lake is fished freely and the proportion of marked fish in the catch used as a basis for calculation of the total population of the lake. Copper Lake was fished uniformly for 12 hours by 8 men, who caught and marked 34 trout, the largest being 33 cm. The lake was then observed for 10 weeks, during which 68 trout were caught, of which 3 had marks. Thus the population is calculated as

$$\frac{68 \times 34}{3} = 771 \text{ trout in the lake.}$$

It will be apparent from the equation that the calculated total population is not of high accuracy.

SUPPORTING CAPACITY OF LAKE FOR TROUT

Fry (1951) has summarized the work in his laboratory and elsewhere regarding the effect of the environment on the metabolism of *Salvelinus fontinalis*. Documentation for the following statements will be found in his paper. It appears that trout are tolerant of such a wide range of pH in nature that hydrogen ion concentration is not a ruling influence, and the same may be said of carbon dioxide. While the response of trout to hydrostatic pressure has not been investigated, they are in general confined to depths of less than 45 feet in lakes. There is no evidence that their survival depends upon the intensity of light in lake waters. Since the species migrates from fresh water to the sea, it appears unlikely that the slight changes of salt concentration found in lakes will require consideration either. This analysis leaves temperature and oxygen as the variables on which to fix attention when considering trout waters.

On oxygen and temperature, Fry's results are more precise than any previous ones and allowance is made for acclimation of the trout prior to testing. With his values at hand it becomes possible to attempt an assessment of the water suitable for trout in Copper Lake at different times of the year. The temperature limits for full activity range from 14° to 19°C. The limits at which activity is cut to 50 per cent are obtainable from an examination of figure 3 in a paper by Graham (1949). The information concerning limits for temperature and oxygen requirements is summed up in Table II.

By making use of this information it is possible to describe Copper Lake with reference to habitability by trout at different times of the year. Figure 2 has been drawn so that its total area represents a unit which might be called 100 volume-years. The areas of the parts represent the numbers of volume-years which support trout at various levels of metabolism. To construct the figure, the volume of the lake was established by measurement and plotted as the ordinate with an arbitrary value of 100. The body of the graph covers an interval of one

TABLE II. Oxygen and temperature limits for activity of fully acclimated trout. Data of Fry and Graham.

	Temperature	Minimal oxygen
	°C.	*ml./l.*
Scope for full activity; incipient limiting values	14–19	5.6
Limits for 50% activity	6–24	3.9
Lethal limit	25	0.6

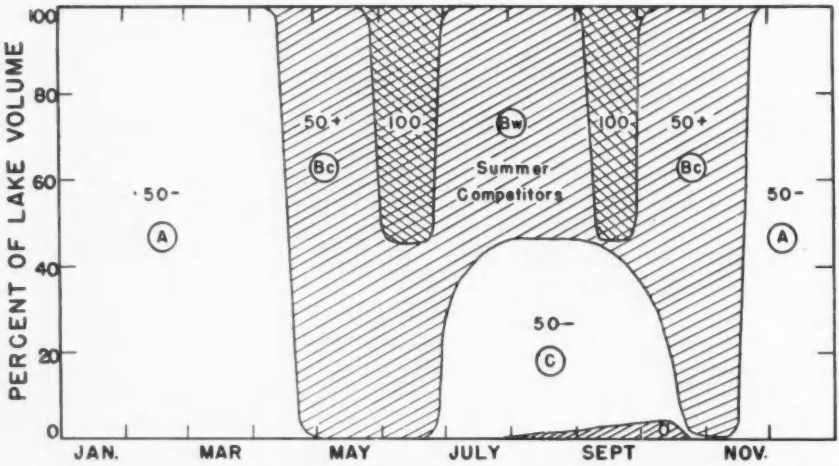

FIGURE 2. Habitable trout water in Copper Lake in relation to time of year and level of activity. The volume of the lake is called 100, hence the area of the chart might be called 100 volume-years. The meaning of the symbols is explained in the text and summed up in Table III. The subscripts *c* and *w* should be read as "cold water" and "warm water".

year. Many summer temperature and oxygen observations on Copper Lake have been made, but winter data on the attainment of 6° and 14°C. are more scanty and have been supplemented by other information. The times of attainment of 6° in the spring and the decrease to 6° in the autumn have been derived from records of the Halifax Public Service Commission, and are based on average temperatures for several years taken 20 feet below the surface of a lake in the Halifax Water Supply. Further data on lake temperatures were taken from the work of Smith (1952) in New Brunswick. Supplementary information on the attainment and lowering of temperature to 14° by the LaHave River over several years was obtained from Hayes (1953). There are also numerous summer observations on other lakes in Nova Scotia made in this laboratory. All this information has been brought together to construct Figure 2 and Table III.

The areas designated "A" at the ends of Figure 2 represent the winter season during which the temperature of the water is below 6° so that trout

TABLE III. Areas of Figure 2 permitting various levels of trout metabolism.

Designation on Fig. 2	Capacity for active metabolism	Cause	Relative vol.–years (total lake is 100)	Absolute vol.-years	Vol.-years per acre
				10^4 *cu. m.*	10^3 *cu. m./acre*
100	Maximal		8	9	1.7
B_c	Above 50%	Below 14°	28	34	6.3
B_w	Above 50%	Above 19°	11	13	2.4
A	Below 50%	Below 6°	41	49	9.1
C	Below 50%	Lack of O_2	12	14	2.6
O	Lethal	Lack of O_2	0.5	0.6	0.1
TOTAL			100	120	22.2

activity might be expected to be reduced below the 50 per cent level. The areas "B_c", of which there are two, are limited by the spring and autumn attainment of 6°. Above 6° the activity of trout would be 50 per cent or more of its maximal. (Temperatures above 24° which are occasionally encountered at the surface on hot summer afternoons may be neglected.) Within the 50+ region there will be short intervals during which some of the water in the lake is capable of supporting trout at full metabolic capaoity. These are the two areas labelled "100" on Figure 2. They represent the fraction of the water and the fraction of the year during which the temperature lies between 14° and 19°C. and the oxygen supply is above 5.6 ml. per litre. Here the trout can live on even, or better than even, terms with its competitors. The section B_w in the centre of Figure 2 is brought about by a warming of the epilimnion above 19°. The area "C" represents an interval during the summer when the oxygen below the thermocline is too small even to permit 50 per cent activity. Finally there is a negligible zone where oxygen is too low to support trout life, as shown in the area marked "O" at the bottom of Figure 2.

From a study of several other lakes in Nova Scotia and from an examination of data on New Brunswick lakes (Smith, 1952) it appears that the conditions indicated in Figure 2 are quite general for stratified lakes in this area. This is to say that there is commonly no water available in summer permitting full activity of trout.

The volume-year values are given in Table III, which shows that the zone for full activity constitutes 8 per cent of the total for the lake. The final two columns of Table III are absolute values which have been included to facilitate comparison with other lakes.

In summer trout would be expected to retreat from the surface and take up

a position just above the area "C" where temperature is ideal and oxygen not too low. The effect of the partial-poisoning experiment to be described was the elimination of certain species occupying the area B_w which has been labelled "summer competitors" in Figure 2. These species evidently were restricted in mid-summer to the poisoning zone near the shore. The area constitutes 11 per cent of the total volume-years and might become effectively available to trout. This is to say that trout at 50 per cent activity might be able to take up the available niche for carnivores if summer competitors were eliminated. It is not necessary to suppose that the trout would occupy the territory in summer, although they might well conduct brief forays into it for feeding. The extra forage material (*Fundulus* and invertebrates) left by their former competitors could be consumed when more suitable temperatures arrived in autumn. If one imagined this to be so, then the capacity for trout following a partial-poisoning experiment might be arrived at by the fraction $(11 + 8)/8 = 2.4$ times the former level. This would be the expected improvement from enabling trout to utilize the nutritive capacity now used by warm-water competitors.

The poisoning experiment would hardly be expected to permit the trout to enter, with advantage, area "C" where oxygen is lacking. It might be thought that elimination of warm-water carnivores would benefit trout in the areas "B_c" and even "A". We are inclined, however, to think that here the capacity of the trout to forage is limited by its own reduced activity metabolism (Fry, 1947) rather than by the presence of warm-water fish. These would have their winter metabolism reduced to an even greater extent than trout, scarcely doing more than holding on in a state of hibernation. If the reasoning in the preceding paragraphs is correct, it would suggest that a poisoning experiment of the kind undertaken could be expected to yield only a limited improvement in Copper Lake and similar lakes of medium to low productivity. A greater percentage improvement would follow if the "100" zones were smaller, as in a warmer climate, although at the same time the season for successful angling would also be shorter. One would expect the absolute improvement to be greater in lakes of higher productive level, since there would be more trout competitors to eliminate.

CONDUCT OF THE EXPERIMENT

The experiment included stocking of the lake accompanied by a creel census, and poisoning of the shallows accompanied by a shore and brook census on the day following. These procedures will be described in turn.

During a total of seven years the lake was stocked by the Fish Cultural Development Branch with fingerlings or occasionally yearlings. The fish introduced into the lake were marked by finclipping, usually the adipose fin and one other being removed. A creel census was maintained on the lake in the course of which a record was made of the lengths of all trout caught and whether fins were missing. No special effort was made to stimulate angling, and there is no evidence of a change in angling intensity during the study.

The poisoning experiment consisted of adding ground derris root, said to

contain 5.1 per cent of rotenone, to the portions of Copper Lake out to the 3-metre (10-foot) contour line. The powdered poison was mixed with water to about the consistency of malted milk and applied with the type of pack spray used to combat forest fires. Sprays were used both from boats and by workers wading into the shallow areas. In the preliminary mixing a weighted quantity of derris powder was added to a large metal pail with a quantity of domestic detergent, and the whole was beaten up with water until no solid lumps remained.

Before application began, the 3-metre depth contour, known approximately from surveys of the lake, was sounded out and marked with buoys. The area of the 3-metre zone was some 5.6 hectares, with a volume of 8.4×10^4 cubic metres. 48 kg. of derris dust were added, giving a concentration of 0.57 parts per million in the experimental area. The recommended lethal dose is 0.5 p.p.m.

The fish started to die almost immediately after the poison was added. By the following morning it was evident that all were dead that were going to die, and counting was begun. For this the shore was divided into 5-metre lengths and every fifth length examined carefully. All fish were picked up and their standard lengths in mm. recorded. Except for the first year of the poisoning, all fish were also weighed. Only fish which were washed up on the shore were considered; it is believed that these constituted the best available approximation to a constant fraction of the fish killed. However, no guarantee of this exists, and the results may well be affected by differences in shape, specific gravity and rate of decomposition between various species.

In the partial poisoning of Copper Lake it was hoped to kill coarse fish selectively by poisoning the shallows, while the trout remained in the cooler depths. During the whole five years of the experiment only one trout was observed to be washed ashore following poisoning. Thus the results may be considered successful.

Poison flowing into the outlet stream killed fish for one-quarter to one-half mile down. A survey was made of the stream and the dead fish were counted and measured.

No systematic estimate of the effect of poisoning on organisms other than fish was attempted, but large numbers of dead leeches drifted to the lee shore, while the abundant Unionidae and aquatic snails were not noticeably affected.

It was not determined how deeply the poison penetrated, how long it retained its potency or what proportion of fishes in the lake were killed, but approximately twenty-four hours after completion of poisoning, schools of live *Fundulus* were observed in the shallows.

RESULTS OF THE EXPERIMENT

The fish which were observed on the shore the day after poisoning are recorded in Table IV by numbers and in Table V by weights. It will be immediately apparent that there was a great decline in the fish killed by the poison after the first year. The effect of the five-year poisoning experiment may be considered with reference to three groups of fish. First, there were three species—

shiners, perch and chubs—which were evidently eliminated from the lake by poisoning. Two of these, perch and chub, might be considered to be at the same food level as the trout. Three further species—killifish, suckers and eels—were not totally removed by the poisoning, but decreased to a value somewhat below the initial level. These fish would be expected to replenish themselves in the lake as soon as opportunity offered through the cessation of poisoning. There might also be mentioned two species which were negligible for purposes of this experiment, smelt and stickleback. Trout have also been included in Tables IV and V in order to draw attention to the fact that poisoning did not affect them, at least in so far as shore counts were concerned.

A final check was made on the population of the lake in August, 1954, when a gill net and trammel net were repeatedly set at various depths and places

TABLE IV. Numbers of dead fish cast ashore and counted one day after poisoning. Values as shown are counts multiplied by five, since only one-fifth of the shore was actually searched.

	1948	1949	1950	1951	1952
Shiner, *Notemigonus crysoleucas*	8,540	90	15	5	0
Perch, *Perca flavescens*	4,015	20	0	0	0
Chub, *Semotilus atromaculatus*	880	80	0	10	0
Killifish, *Fundulus diaphanus*	3,890	930	190	2,205	1,640
Sucker, *Catostomus commersoni*	2,420	210	140	680	970
Eel, *Anguilla bostoniensis*	310	125	55	105	480
Smelt, *Osmerus mordax*	55	5	5	150	270
Stickleback, *Gasterosteus aculeatus*	25	0	0	0	10
Fingerling trout, *Salvelinus fontinalis*	5	0	0	0	0
Adult trout, *Salvelinus fontinalis*	0	0	0	0	0
TOTAL	20,140	1,460	405	3,155	3,370

TABLE V. Weights in grams of dead fish on the lake shore one day after poisoning. Observed values × 5 as in Table IV. Weights from 1949 on were obtained directly; weights given for 1948 were derived from lengths, using length-weight relationships derived from later years, supplemented by Carlander (1950, 1953).

	1948	1949	1950	1951	1952
Shiner	33,690	210	160	250	0
Perch	18,890	305	0	0	0
Chub	3,470	95	0	185	0
Killifish	5,610	945	530	6,490	2,730
Sucker	40,685	305	640	12,650	5,785
Eel	4,650	1,685	645	4,745	1,440
Smelt	275	5	5	135	243
Stickleback	30	0	0	0	12
Fingerling trout	10	0	0	0	0
Adult trout	0	0	0	0	0
TOTAL	107,310	3,550	1,980	24,455	10,210

during three successive nights. The only fish taken were trout, suckers and eels, none in large numbers. Nothing divulged by the netting suggested that a very large trout population was in existence in the lake; in other words, the netting operation confirmed, or at least did not contradict, the creel census data discussed below. In September, 1954, the shallow portions of the lake were seined. The dominant fish was *Fundulus* and many small suckers were also taken, as well as occasional sticklebacks. From the netting and the seining it appears that the former population of shiners, perch and chubs which disappeared in the final years of the poisoning program is still absent.

It is worth noting, with reference to the quantities of fish killed in different years, that the derris root used was of two batches. One batch was purchased in 1948 and used through 1949 and 1950. In 1951 a new batch was purchased and was used in that year and in 1952. The kill in 1951 was somewhat greater than in 1950, which might be attributed to fresh derris powder, although we have no evidence to suggest that the old powder had deteriorated through storage, and so far as was known it had not been subject to dampness or otherwise injured. There are other variables which might have accounted for the difference between 1950 and 1951. For instance, the direction in which the wind was blowing might carry dead fish or derris powder from the shallows out into the centre of the lake, thus affecting the shore count next day. In these matters no two years were precisely alike and effects arising from weather conditions might be more important than variations in the poisoning power of the derris root.

A careful survey of the outlet stream was made, through the killing zone down to where healthy fish were observed, a distance of one-quarter to one-half mile. There is a marked variation in stream conditions leading from the lake. For some little distance downstream the water is warm because of run-off from the lake and because the stream is not densely covered by bushes. Beyond this the stream is shaded and the water is noticeably cooler. The water remains cold to the limits of the poisoning zone, and appears to provide excellent conditions for trout. Farther down, the stream opens into meadow land where the water is somewhat warmer.

The results of the outlet survey are shown in Table VI, from which it is apparent that shiners and perch are absent from the stream. Chubs were found dead only in the warmer part near the outlet from Copper Lake, and they were also observed alive in meadow portions of the stream below the zone poisoned. Evidently they prefer warmer water than that favoured by trout. *Fundulus* was observed only at the immediate mouth where the lake enters the stream, and is scarcely to be considered as a stream fish. The number of *Fundulus* varied from year to year in the counts, depending on whether a school happened to be near the outlet or not. Suckers are found farther downstream than *Fundulus* but not to the trout waters. The smelt and stickleback are unimportant from the point of view of stream economy. This leaves eels and trout as the permanent inhabitants of the cool stream waters. As regards eels, there could be no expectation of reducing their numbers in any systematic way, and so far as the observations go, it appears that the stream was repopulating itself with them. It is of some

TABLE VI. Numbers of dead fish counted in the outlet stream after poisoning. Lethal effects were observed to extend about one-half mile downstream.

	1948	1949	1950	1951	1952
Shiner	0	1	0	0	0
Perch	0	0	0	0	0
Chub	10	35	19	0	0
Killifish	0	2	8	65	83
Sucker	0	30	10	50	45
Eel	173	61	43	217	81
Smelt	0	0	0	1	0
Stickleback	0	2	0	0	1
Fingerling trout	11	76	40	92	267
Adult trout	0	8	9	91	102
TOTAL	194	215	129	516	579

interest that in the final year of the observations, 1952, eels were found only in the warmer waters not populated by trout, whereas in the earlier years the eels were observed to extend through the trout waters. One may speculate whether the poisoning experiment could have reduced the population pressure on eels so that they were no longer pushed into the cool trout water but selected the warmer waters of the lake and stream.

The marked increase of trout in the outlet stream was the most spectacular feature of the whole experiment. The increase was steady and consistent; it applied to both fingerlings and adult trout; and it resulted in a twentyfold increase in the number present. Indeed, adult trout were actually absent at the beginning of the experiment. It is evident that the trout population in the area is adequate to repopulate this section of the stream to pre-poisoning levels. Incidentally, no marked hatchery fish was ever picked up in the outlet stream survey. Referring to the statement above that eels were found in the trout waters of the stream during the first years of the poisoning but not later, it appears reasonable to suppose that the increased trout population replaced eels.

ANGLING SUCCESS

During the years 1944 and 1945 and again during four years of the poisoning program, the lake was stocked with fish from the Antigonish Hatchery. The stocking program is shown in detail, together with information on angling success, in Table VII, columns 7 to 10. The planted trout were marked by fin-clipping. In three of the four years of stocking (1949–1951), clipping included the adipose fin which is less likely than others to regenerate subsequently (Smith, 1952). In order to make allowance for possible regeneration, all fish reported with fins missing have been included in the returns as stocked fish.

The discussion of Table VII might conveniently begin with column 5. The yield of trout prior to the poisoning experiment and during its early years was fairly uniform at about 0.7 pounds per acre. In the final year of poisoning, 1952,

TABLE VII. Stocking program and angling success in Copper Lake. Pre-poisoning data from Smith (1948). Smith used 40 acres as lake area, hence his column 5 values are changed to correspond to newer measure of 54 acres.

	Anglers' catch					Marked trout planted		Marked trout caught	
1	2	3	4	5	6	7	8	9	10
Year	Total number	Number per rod hour	Ounces per rod hour	Pounds per acre	Average length (inches)	Number	Size (inches)	Number	Percentage of total catch
				PRE-POISONING (AFTER SMITH)					
1944						2600	2½–3		
						520	4½–5		
1945	326	0.5	1.0	0.7	6.7	260	6+	72	22.1
1946	309	0.8	1.8	0.8	6.6			17	5.5
1947	159	0.3	0.7	0.4	6.8			0	0
				ANNUAL POISONING FROM 1948 TO 1952					
1949	147	0.5	1.9	0.7	7.6	2600	2½–3	0	0
1950	122	0.6	2.9	0.7	8.2	2600	2½–3	3	2.5
1951	175	0.6	1.4	0.5	7.0	2600	2½–3	5	2.9
1952	174	0.4	2.3	1.1	8.5	2600	4½–5	3	1.7
				POST-POISONING					
1953	212	0.3	1.8	1.3	8.5			1	0.5
1954	196	0.4	3.4	1.8	9.7			1	0.5

and in the two subsequent years of census-taking there was a perceptible increase in the yield. If the maximal effect of the poisoning was achieved by 1954, the result of the treatment, expressed as a fraction of the former catch, would be $1.8/0.7 = 2.6$ fold.

At first glance the results just described appear to be contradicted by those shown in column 2 of the Table, which shows that there was no increase in the number of trout caught by anglers. However an inspection of column 6 which shows an increase in average length, together with column 4 which shows the weight of trout caught per rod-hour, clarifies the matter. It is evident that, although the number of trout in the lake did not increase, the average length and weight did. The effect of the poisoning seems to be an improvement in the food situation for the trout.

The effect of stocking the lake with hatchery fish is shown in columns 9 and 10 of Table VII. The returns from hatchery stock were uniformly low except in 1945, the one year when trout over six inches in length were planted. Our results are in agreement with those reported by Smith (1952) for New Brunswick lakes. The conclusion seems to be that Copper Lake, like other lakes in the region, is carrying as many fish as it can under prevailing ecological conditions, and will not be assisted by the planting of additional fish from the hatcheries.

CONVERSION OF PREDATOR BIOMASS

At the beginning of the experiment it was thought that the trout population was being held at an artificially low level by angling pressure. Trout would be angled for preferentially, with the result that competitors, such as perch, would increase at their expense.

The species which are equivalent to trout in the Copper Lake food chain are the eel, the perch and the chub. There is no fish clearly occupying a higher trophic level. The eel is commonly regarded as a predator of trout under natural conditions, but there is little published evidence on the question. According to Smith and Saunders (1955), few trout have been found in the stomachs of eels from Crecy Lake, N.B. However, scars from eel attack, characteristically found just in front of the vent, were noted upon some of the yearling and older trout when angled. Eel predation in Crecy Lake is taken by Smith to be without question, and he attaches considerable significance to the fact that eels spend more years in our lakes than the life span of most freshwater fishes including trout. On the other hand, such stomach analyses of norther hemisphere eels as are available of the European, not the American, species suggest that the eel occupies a slightly lower predation level than the trout (Frost, 1946; Hartley, 1948). The recent study by Burnet (1952) on the diet of *Anguilla diefenbachi* in New Zealand indicates that "trout" (*Salmo trutta*?) are eaten by eels over 28 inches (71 cm.) long and form a major portion of the diet of individuals three feet (92 cm.) or more in length. Few, if any, Copper Lake eels attain a size of 28 inches and it seems likely that they occupy a trophic level which changes with age but is not very different from that of *Salvelinus fontinalis* when the total populations of both species are considered.

The largest suckers may occupy a position in the food chain similar to that of trout, but they are so few it is safer to consider the sucker population in the next lower level. Confirmation of such a view is provided by an experiment of Rawson and Elsey (1948), who attempted to improve rainbow trout survival in a mountain lake by reduction of the sucker population. Suckers were extensively removed by gill nets, traps and seines, and although their weight was reduced to less than half its initial value, there was no detectable improvement in trout survival during the five years of removal or in the three succeeding years.

As to perch, there can be little question about its rough equivalence to trout. Both subsist on a mixed animal diet in which fishes become more important with age (Adams and Hankinson, 1928; Metzelaar, 1929).

In order to examine the effects produced in the species composition of the top predator level it is necessary to have figures for the change in mass of each species. For the trout, the angling and marking experiment provided an estimate of the number of fish in the lake before poisoning. The estimated number was 771, with a large sampling error. The marking experiment did not provide a measure of trout mass, but its result can be converted to mass by applying to it the average size of Copper Lake trout as known from the creel census. This gives a figure of 85 kg. for the initial trout mass. The reliability of the figure is low, but it is of the proper order of magnitude. Except for the creel census results, there are no data available concerning the final mass of trout.

An estimate of the change in perch mass may be obtained from the poisoning figures. During the first year 19 kg. and during the second 0.3 kg. of perch were washed ashore. In later years no perch were killed. It appears from this that a total kill of the resident perch population was affected. Since the second year kill is a second-order correction to that of the first year, the total perch washed ashore may be taken as 19 kg.

A certain proportion of the fish killed must have sunk to the bottom, so that this estimate of the initial perch population is too low. Ball (1945) has found, in a marking and poisoning experiment in Michigan, that about 60 per cent of poisoned bluegills floated ashore. Applying this percentage to our results, we get an initial perch mass of about 32 kg. The final perch mass is, of course, zero, so the net decrease is 32 kg.

The same procedure applied to the chub figures, using Ball's correction factor of 45 per cent obtained for trout, instead of his 60 per cent figure obtained for bluegills, gives a net decrease of 8 kg. for chub.

Inspection of the poisoned-eel counts indicates that no consistent reduction in the mass of eel has been produced by poisoning.

Considering this food level as a whole, then, we find that there has been a decrease, in chubs and perch, of about 40 kg. If the trout replaced perch and chub on a quantitative basis, one would expect a post-poisoning trout population of $85 + 40 = 125$ kg. That is, the trout population would be expected to be increased to 150 per cent. This value is probably somewhat too high, because the experiment produced a net reduction in the mass of forage fishes which would tend to reduce the net size of the top predator level during the poisoning years.

Once poisoning ceased, the large breeding stock of suckers and killifish would rapidly expand, restoring the forage-fish population to its pre-poisoning mass, with an age structure which would be particularly subject to trout predation. By this time, however, the eel population would be free of the burden of annual poisoning and would be able to claim its share of the mass which has been given to trout in the above calculation. For these reasons the result is likely to approximate an upper limit for trout increase. Although such an approximation is crude and must be regarded as little more than an indication of order of magnitude, it is clear that a very great increase in the standing crop of trout is not to be expected as a result of removing chub and perch.

DISCUSSION

If partial poisoning removed a constant fraction of the fish in the lake and was unaccompanied by recruitment from outside, the population and the annual kill would decline logarithmically during successive years. Conditions are not likely to be so simple. In the first place, the survivors of each poisoning grow during the year, so that the rate of decline in mass will not be as great as one would anticipate from the initial population and the percentage kill. In addition, some species of fish are late spawners, and the surviving individuals might produce a new generation which would partly or completely make good the poisoning loss of each year. This factor is important because the capacity for survival and reproduction tend to increase as the population density declines. If the species has a sufficiently short maturation time, it will decrease under poisoning only until it reaches the point where the annual survivors are able to recoup the loss, and the population will thence exhibit annual fluctuations about a mean.

All of the species are at least potentially capable of repopulating the lake through the outlet stream. For some species, such as the eel, outlet recruitment is of the greatest importance. In Copper Lake the annual kill of eels has been maintained at a more or less constant value almost equal to the first year. The fraction of the existing eel population killed by each application was probably not large. Eels range over the lake bottom and only a part of them would be in the shallow zone and subject to poisoning.

Although *Fundulus* occupies the poisoned part of the lake, many were able to survive the annual treatments, possibly because a substantial part may be in open water beyond the 3-metre contour and possibly because of a high resistance to derris. In most years it was possible to see apparently healthy schools of *Fundulus* in the shallows on the day following poisoning. The killifish has a long spawning season (Thorpe, 1939) and a short maturation time. Survivors of 1948 would be able to spawn before the 1950 poisoning (Thorpe, 1939; Smith, 1952) and possibly even before the 1949 poisoning. This species is in an ideal position to recoup the annual loss and does so.

The sucker spawns early in streams, a habit which ought to provide a supply of young-of-the-year from the inlet stream to repopulate the lake after each poisoning. This however, hardly accounts for the number of large suckers entering

the poison kill in later years of the experiment. There does not seem to be any specific resistance of suckers to rotenone, for they were never observed alive in the later stages of poison application. It appears possible that the sucker ranges freely through the hypolimnion during the summer as suggested by the work of Greenbank (1940) already referred to.

Shiners, perch and chub, all spring spawners in the lake, appear to have decreased exponentially to the vanishing point. Trout, smelt and stickleback were not present in appreciable numbers in the poisoned zone, and so do not enter into the present consideration.

In Table VIII are summed up the results, expected and observed, of the poisoning experiment. Since all the competitors of trout except *Anguilla bostoniensis* were eliminated from the lake, there is no reason to suppose that a total poisoning experiment followed by restocking with trout and *Fundulus* would have given any greater increase than the partial one undertaken. Table VIII contains three independent estimates of the effect. First, on the assumption that trout could enjoy exclusive rights as carnivores of the warm surface waters, provided the inhabitants of these were eliminated, the improvement would be to 240 per cent. Second, assuming that the carnivores killed by poisoning were replaced by trout, the increase would be to 150 per cent. The remaining ratios are all dependent on the creel census, giving ratios from 1.6 to 2.9 with an average of 2.3. In general then, the population of trout might be doubled by poisoning, and this expectation would seem to apply to many lakes of our region. Naturally if trout had been totally fished out before the start of the

TABLE VIII. Observed or expected effect of poisoning on mass of trout in lake.

Basis	Ratio
1. Volume of habitable water	2.4:1
2. Population census, 1947, and assumed replacement by trout of coarse fish killed	1.5:1
3. Pounds per acre angled, average 1949–1954 compared with pre-poisoning average 1945–1947	1.6:1
4. Ounces per rod-hour, average 1949–1954 compared with average 1945–1947	1.9:1
5. Pounds per acre angled, 1954 (two years after poisoning) compared with pre-poisoning average 1945–1947	2.9:1
6. Ounces per rod-hour, 1954, compared with average 1945–1947	2.9:1
7. Average of 3, 4, 5 and 6	2.3:1

experiment, the *ratio* of increase would be infinite. However, as to the absolute number of trout appearing after poisoning, there is no reason to suppose that it will surpass good untreated lakes in the area.

This experiment has shown that by partial poisoning it is possible to replace chub and perch by trout, but that by doing so only a small increase in standing crop of trout will result. This finding might have been deduced from the quantitative nature of a food chain, as established by Lindeman (1942). It is only an example of the general truth that it is very difficult to increase the productivity of the earth, and that the harvestable crop is likely to be materially increased only by harvesting it at a lower level of the food chain. If, as among trout anglers, there is a predisposition against shortening the food chain, then the harvestable crop can be materially increased only by removing organisms other than man which prey upon it.

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